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# A taxonomic revision of the Palaearctic species of the ant genus *Tapinoma* Mayr 1861 (Hymenoptera: Formicidae)

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## Abstract

A taxonomic revision of the Palaearctic species of the ant genus *Tapinoma* Emery 1861 is provided. Due to the extreme rarity of discernable characters, the female castes of 64% of the species are not separable by primary visual perception of an expert and are thus truly cryptic. The main working rationale of the revision is Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT) with formation of species hypotheses largely based on exploratory data analyses and checking these hypotheses by discriminant analysis. NUMOBAT data of all considered species comprise 648 worker samples with 2014 individuals and 30,000 primary data. Species are depicted by z-stack imaging in three standard visual positions. Numeric data on 15 phenotypical characters are presented in comparative tables and supplementary verbal descriptions are given. Analysis of nuclear DNA was based on evaluation of 15 microsatellite loci in 274 nest samples. The NUMOBAT-based classification of eight species of the *Tapinoma nigerrimum* and *T. simrothi* group which are inseparable by subjective visual inspection was confirmed by nuclear DNA data in 98.3% of 169 samples where both morphological and nuDNA data were available. The three cases of disagreement between NUMOBAT and nuDNA classification were discussed. Excluding Nomina Nuda and unavailable names, the revision recognized 34 available names which divide into 21 valid species, 11 junior synonyms and two names placed under Incertae Sedis. Four species are described as new: *Tapinoma hispanicum* **n. sp.**, *T. insularis* **n. sp.**, *T. dabashanica* **n. sp.** and *T. sichuense* **n. sp.** The following synonymies were stated: *T. collina* Foerster 1850, *T. erraticum platyops* Emery 1925 and *T. erraticum bononiensis* Emery 1925 as synonyms of *T. erraticum* (Latreille 1798); *T. tauridis* Emery 1925 and *T. breve* Emery 1925 as synonyms of *T. glabrella* (Nylander 1849) that is erected to species level; *T. minor* Bernard 1945 as synonym of *T. simrothi* Krausse-Heldrungen 1911; *T. simrothi azerbaidzhanica* Karavajev 1932 as synonym of *Tapinoma karavaievi* Emery 1925 that is erected here to species level; *T. erraticum ambiguum* Emery 1925 as synonym of *T. madeirense* Forel 1895 and *T. emeryanum* Kuznetzov-Ugamsky 1927 as synonym of *T. sinense* Emery 1925. Despite an insufficient separation of the female castes of *Tapinoma madeirense* and *T. subboreale* Seifert 2011 by NUMOBAT characters and detection of a hybrid zone in southern France, the heterospecific status of the two taxa was maintained based on sufficient differences in male genitalia and of nuclear DNA over a larger geographic scale. *Formica caerulescens* Losana 1834 is removed from genus *Tapinoma* and recognized as member of the subfamily Formicinae.

**Key words:** cryptic species, numeric morphology-based alpha-taxonomy, integrative taxonomy, nuclear DNA

## Introduction

Ants of the genus *Tapinoma* Foerster 1850 have repeatedly attracted the interest of myrmecologists and, increasingly, of pest exterminators in settlement areas and crop fields. Their fighting and interference behavior recurrently stood in the focus of consideration. The defensive secretion produced by the anal gland which is highly poisonous to probably all ant species, is a mixture of ketones and a dialdehyde and polymerizes if sprayed on the cuticular surface of an enemy which prevents the evaporation of the toxic ketones (Blum & Hermann 1978). Negative furor has been produced after the turn of the millennium by supercolonial ants of the *Tapinoma nigerrimum* species complex, which became massively invasive in the Benelux countries, Switzerland, France, Germany and fragile Mediterranean islands such as Corsica, causing here havoc within human settlements and other urban areas. Substantial costs are generated in municipal areas by sinking of pavement, curbsides and other building structures that are undermined by the massive soil ejection activity of these ants. Their supercolonies exterminate nearly all autochthonous ant species, may occur as pests in horticultures, foster populations of scale insects and aphids, their sheer numbers are a nuisance to humans and their eradication is most difficult (Heller 2011, Mansour *et al*. 2012, Nordijk 2016, Seifert *et al*. 2017, Van Boesschoten 2017, Seifert 2020a, Dijk *et al*. 2022, Gouraud & Kaufmann 2022, Centanni *et al*. 2022). At least two of the invasive species may forage at ground temperatures of 3 to 7°C and at least one species shows a high frost resistance. Ants of the *T. nigerrimum* complex are known from Corsica and southern France to limit the spread of the invasive Argentine Ant *Linepithema humile* (Mayr 1868). In space and food competition assays of Blight *et al*. (2010) ants of this species complex appeared to be more efficient than *Linepithema* in both interference and exploitative competition, clearly superior in direct fighting, dominated food in 100% of the replicates after one hour, and invaded *Linepithema* nests while the reverse was not observed.

The recent fauna of the ant genus *Tapinoma* Foerster 1850 is currently believed to contain 72 valid species and 22 valid subspecies with about 80% of the recognized taxa occurring in tropical zones of the Old and New World (Bolton 2023). There is no modern worldwide taxonomic revision of the genus using testable data sets and the high number of truly cryptic species, at least in the Palaearctic fauna (but certainly also globally) represents an

enormous challenge. Seifert (2009) defined truly cryptic species as "...species which are not separable by primary visual or acoustic perception of an expert. This reflects the immediate sense of the word and restricts such species to truly cryptic cases—i.e., to species not safely separable by training of innate pathways of the human cognitive system. Rather, their reliable identification requires the application of elaborate methods such as numeric recording and analysis of phenotypic characters, DNA analysis, biochemistry or analysis of sound spectograms." Palaearctic *Tapinoma* ants are in fact extremely poor in discernable characters: the position and number of the very few setae are uniform across the species, there are no obvious differences in length, distribution and density of pubescence and significant differences in cuticular microsculpture do not exist. Furthermore, allometric changes of shape characters obscure really existing differences and pigmentation is tediously homogenous. According to the experience of Seifert, there is no group of Palaearctic ants with so weak interspecific differences in external phenotype.

The multitude of interesting biological properties, which are also relevant for humans from an economic point of view, generates an interest for an in-depth taxonomic study of these ants that solves the species-separation dilemma. A first step in this direction has been done by Seifert *et al.* (2017) who separated the *Tapinoma nigerrimum* complex into four species three of which may form huge supercolonies. These discoveries became possible after the development of high-resolution methods of Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT) in which Nest Centroid Clustering (Seifert *et al.* 2013) plays a central role in formation of species hypotheses. Yet, remembering several treacherous cases of discrete intraspecific dimorphism (Seifert 2016, Seifert 2019a, 2019b) and the high incidence of interspecific hybridization in ants (Seifert 1999, Steiner *et al.* 2011, Seifert 2021, Weyna *et al.* 2022, Satokangas *et al.* 2023), species hypotheses formed by NC-clustering have always to be checked by analyses displaying results in the simple vectorial space such as principal component analysis. Yet, even a carefully done morphological investigation may lead to wrong conclusions when there is no information provided by independent data sources. The best approach, aiming at the two strongest indicators of species identities and avoiding too many methods being involved, is a combination of high-resolution NUMOBAT and analysis of nuclear DNA. This follows the logic of the GAGE species concept (Seifert 2020b) according to which species are defined as separable clusters of nuclear genes and / or of their expression products. Using this approach, this paper intends to bring more clarity into the chaos of 35 available names many of which had been generated in the past by prolific description of variants.

## Material

This revision is largely worker-based with consideration of morphology of male genitalia and nuclear DNA. NUMOBAT data of the species groups considered in this paper comprise 648 worker samples with 2014 individuals and 30,000 primary data. With the exception of type specimens and other samples of special relevance, data of this material are not presented in detail in the main text of this paper but listed up in the electronic supplementary information SI1 (worker individuals), SI2 (nest sample means of workers). A smaller data set providing information on genital characters of 102 males is given by supplementary information SI3. The abbreviations of type depositories are as follows:

FMNH Helsinki—Finnish Museum of Natural History, Helsinki / Finland
HMNH Budapest—Hungarian Museum of Natural History Budapest, Hungary
MCSN Genova—Museo Civico die Storia Naturale Genova, Italy
MCZ Cambridge—Museum of Comparative Zoology of the Harvard University, Cambridge, USA
MHN Genève—Muséum d'histoire naturelle de Genève, Genève, Switzerland
NHM Basel—Naturhistorisches Museum, Basel, Switzerland
NHM Wien—Naturhistorisches Museum Wien, Wien, Austria
SMN Görlitz—Senckenberg Museum für Naturkunde, Görlitz, Germany

Data on nuclear DNA (microsatellites) were analyzed in 274 nest samples (for details see supplementary information SI2).

**Methods**

**The applied species concept**

The GAGE species concept (Seifert 2020b) is used here. It states that species are separable clusters defined alone by nuclear genes and/or their expression products. The morphology investigated here is such an expression product whereas microsatellite markers represent nuclear DNA. The concept requires to test taxonomic hypotheses by exploratory and hypothesis-driven data analyses and using the threshold principle to evaluate evolutionary divergence. Yet, this approach was not applicable in 10% of the species considered in this revision as these were represented by only single nest samples. Here we had to content ourselves with assessing if their NUMOBAT data, shape and surface structures were outside the range of variation of the next similar species with sufficient sample size.

**Equipment and measuring, character definitions, data analyses and classification**

**Equipment and measuring**

A pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0x planapochromatic objective (resolution 1050 lines/mm) was used for spatial adjustment of specimens at magnifications of 120–360x. A Schott KL 1500 cold-light source equipped with two flexible, focally mounted light-cables, providing 30°—inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarized-light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52 % of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. Z-stack images of mounted specimens were produced with a KEYENCE VHX-7000 digital microscope using magnifications between 80 and 700x.

**Definition of morphometric characters**

Fifteen primary measurements were taken in workers (CL, CW, dAN, EL, ExCly, ExClyW, ExOcc, Fu2L, Fu2W, MGr, ML, MW, nExCly, PoOc and SL). In bilaterally developed characters, arithmetic means of both body sides were calculated. All measurements were made on mounted and fully dried specimens. Measurements of body parts always refer to real cuticular surface and not to the diffuse pubescence surface. The reproducibility of NUMOBAT data recording in general is strongly dependent from carefully considering the character definitions. In very small structures such as morphometry of the 2nd funiculus segment, the resolution of the microscope and illumination of the object are also important.

**CL**—Maximum cephalic length measured between points A and B; A is the posteromedian margin point of head capsule; B is an imagined median point situated at the same transversal level as the most anterior points of clypeus left and right of clypeal excision. Bilateral asymmetries are averaged.
**CS**—Cephalic size with CS=(CL +CW)/2.
**CW**—Maximum cephalic width.
**dAN**—Minimum distance of the inner (centripetal) margins of antennal socket rings which is best measurable in dorsofrontal view (Fig. 1)
**EL**—Eye length; maximum diameter of the compound eye over all structurally defined ommatidiae; bilateral mean.
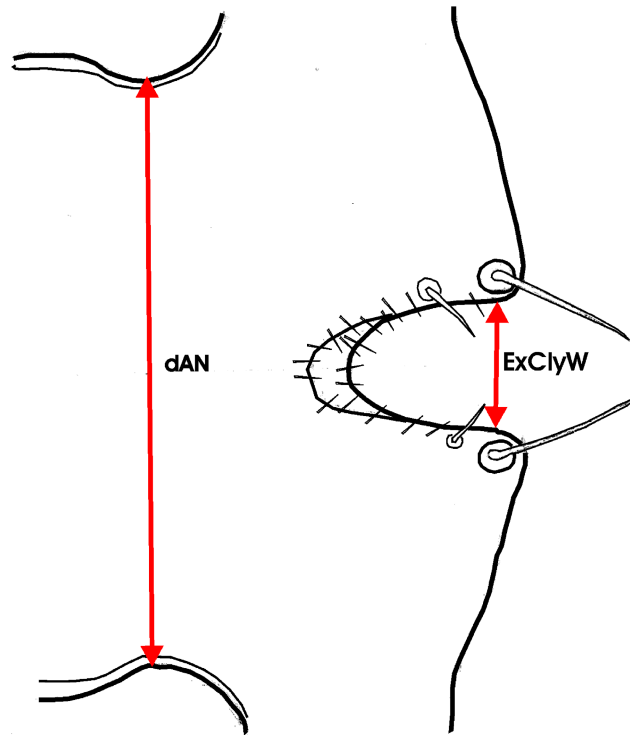
**FIGURE 1.** Measuring width of clypeal excision (ExClyW) and minimum distance of inner margins of antennal socket rings dAN.

**ExCly**—Maximum depth of anteromedian clypeal excision as it appears in frontodorsal view and with median line of head positioned perpendicular in the visual field; bilateral asymmetries are averaged (Fig. 1).

**ExClyL/W**—Ratio ExCly /ExClyW.

**ExClyW**—Width of clypeal excision at the level of the base centres of the two most apical and largest setae (Fig. 1).

**ExOcc**—Depth of excavation of posterior vertex with head in full face view. Procedure: Using high magnification with low depth of focus, adjust the head to the measuring position defined for CL. Focus both posterior corners of vertex until they form a sharp contour, adjust them to equal horizontal level within the visual field and superimpose the corners with the horizontal line of the cross-scale. Change the focal level until the median part of posterior vertex forms a sharp contour. Read the depth.

**Full face view**—dorsal aspect of head adjusted for measuring both maximum CL and CW. Use of high magnifications with low depth of focus improve the correct spatial adjustment.

**Fu2L**—Median length of second funiculus segment in dorsal view. Dorsal view is given when the swiveling plane of $1^{st}$ funiculus segment is positioned in the visual plane. Take care to really measure median length as the segment's sides have unequal length and to recognize the real distal margin of the segment. The latter has a very thin cuticle, frequently producing a narrow, shining ribbon that seems to be, by optical impression, demarcated from the rest of the segment. The median line of the segment is visualized by centre of the patch reflecting the coaxial light.

**Fu2W**—Maximum width of second funiculus segment in dorsal view. Procedure: use the same spatial adjustment of the ant as in measuring Fu2L but rotate it in the visual plane by 90°. Use of transmitted-light is important visualize the real cuticular surface which is often obscured by pubescence.

**IFu2**—Index Fu2L / Fu2W.

**ML**—Mesosoma length from the caudalmost point of lateral metapleuron to rear margin of anterior pronotal fringe (in workers). In workers, if anterior measuring point is concealed, keep the orientation of measuring line, choose a higher magnification, measure from the caudalmost point of lateral metapleuron to the level of promesonotal margin and multiply by 1.415. This factor is an average estimated from several species.

**MGr**—Depth of metanotal groove / depression in lateral view; the upper reference line extends between the highest points of mesonotum and propodeum perpendicular to which depth measuring is performed.

**MW**—Maximum pronotal width.

**nExCly**—Bilateral sum of pubescence hairs and smaller setae protruding a just visibly at magnifications > 200x across margin of clypeal excision. The two large anteriormost setae are not counted (Fig. 1). If there is in the caudal part of the excision a more dorsal blunt margin (thinner line in Fig. 1) in addition to the more ventral sharp margin (thicker line), hairs protruding across the dorsal margin are also counted. This second dorsal margin is typically seen in species of the *T. nigerrimum* complex. The correct count in the example of Figure 1 is 21.

**PoOc**—Postocular distance taken in the same spatial adjustment as in measuring CL: distance from the transversal level of posterior eye margin to median point of hind margin of head; bilateral asymmetries are averaged.

**SL**—Scape length excluding articulatory condyle. Transmitted light is useful to visualize the real distal end of scape that may be obscured by pubescence.


**Terminology of male genitalia**

We follow the terminology used by Yoshimura & Fisher (2011) with the exception of retaining the name "subgenital plate" for the terminal abdominal sternum. The paramere usually consists of a basal part named here basimere (= squamula in the terminology of Kutter 1977) and a distal part named here harpago (= stipes in the terminology of Kutter 1977). The parameres are not in all ant groups separated in a basal and distal part. The digitus is the hook of the volsella (usually the most distal part) while the cuspis is another distal part of volsella (usually subdistal). The aedeagus is the most median genital segment and is named by other authors sagitta or penis valve (Fig. 2). Using the overall impression of genital characters for quick subjective separation of cryptic species is most problematic due to large variability. As in somatic characters of workers, demonstration of species differences is here only possible via standardized morphometrics. The following measurements were taken in ventral view with the ventral surface of the subgenital plate placed in visual plane (Fig. 03).

**dSPST**—Bilateral mean of the longitudinal distance of the transverse levels of the tips of subgenital plate and of the tips of the stipes (harpago).

**SPdT**—Distance of the tips of subgenital plate.

**SPExc**—Depth of the excision of subgenital plate.

**SPWPr**—bilateral mean of width of the arms of subgenital plate at the point where the pubescence hairs fringing the inner margin turn from mediad orientation to caudal orientation—this is slightly caudal of the bottom of excision (Fig. 04).

**STdT**—Distance of the tips of the harpago.
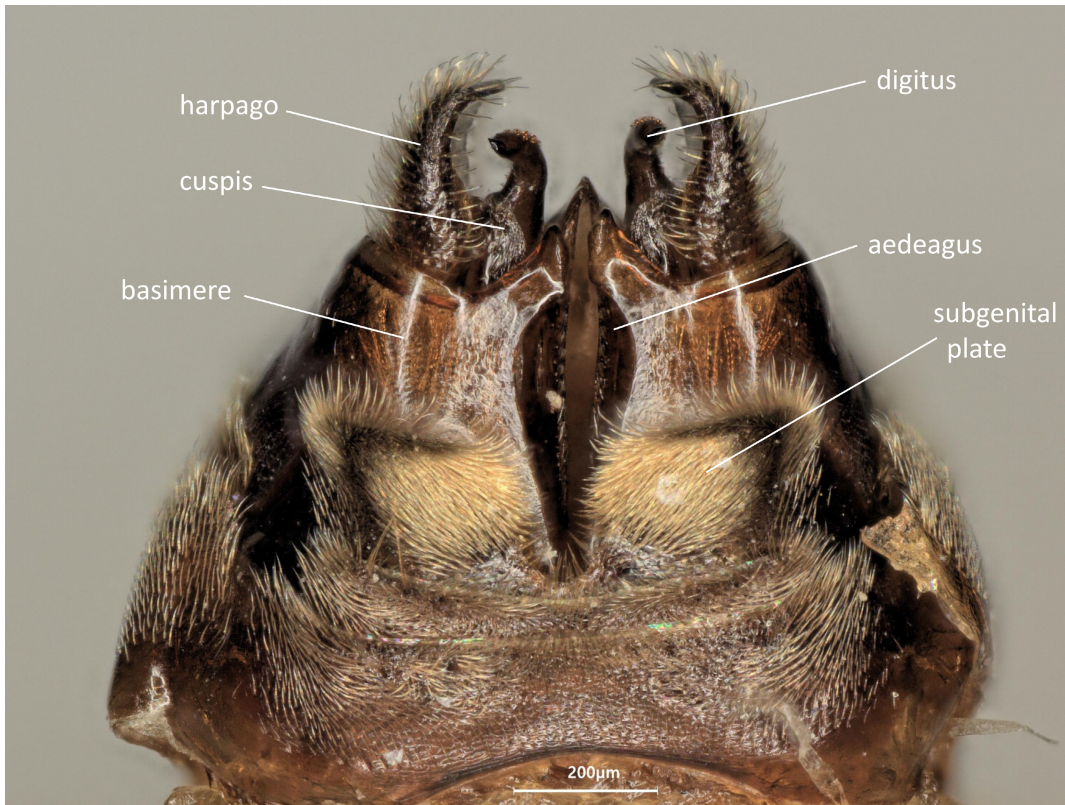
**FIGURE 2.** Terminology of male genitalia in ventral view shown in the example of *Tapinoma glabrella* from Dragonja / Slovenia, 2017.05.15
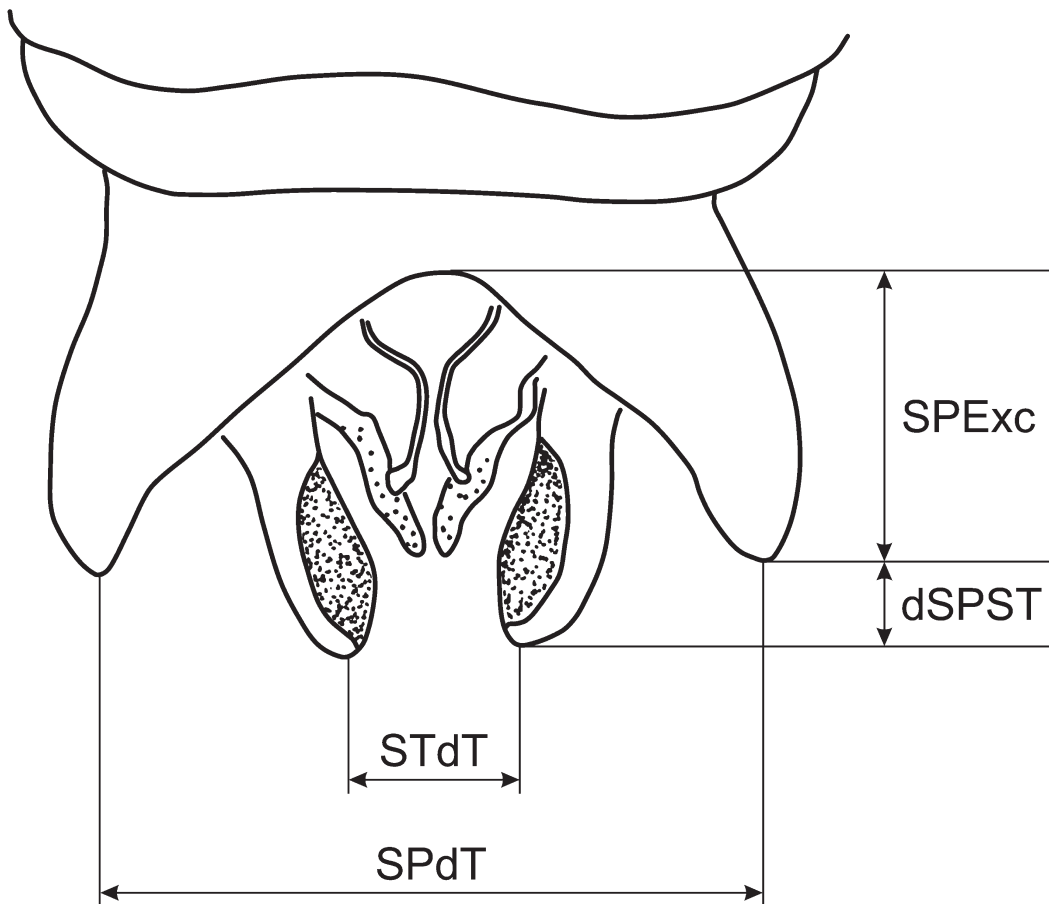


**FIGURE 3.** Four measurements in male genitalia in ventral view

**FIGURE 4.** Measuring the basal width of the arms of subgenital plate in ventral view shown in the example of *Tapinoma subboreale* from Percile / Italy, 2013.06.23

## Removal of allometric variance

Many shape characters in *Tapinoma* are significantly influenced by allometric growth (Seifert *et al.* 2017). This effect is particularly strong in workers of the *T. nigerrimum* complex where cephalic width of the largest majors amounts 225% of the value in the smallest minors. In order to reveal in comparative tables which shape variables do really differ between the species independent from body size, a removal of allometric variance (RAV) was performed with the procedure described by Seifert (2008). Since the evaluation of scatter plots showed differing parameters of allometric functions in small and large workers, RAV was performed by a biphasic linear function with a breaking point at CS = 0.9 mm. RAV was calculated assuming all individuals to have an cephalic size of CS = 0.9 mm. RAV functions were calculated as the arithmetic mean of the species-specific functions of those 14 Palaearctic *Tapinoma* species in which more than 25 worker individuals were available for analysis. The RAV functions of 14 shape and one seta character are given in the following. The variables $ExCly / CS_{900}$, $ExClyW / CS_{900}$ and $MGr_{900} / CS$ are given in per cent.

For specimens with CS < = 0.9 mm:

$$CL / CW_{900} = CL / CW / (-0.4501 * CS + 1.4613) * 1.0572$$
$$SL / CS_{900} = SL / CS / (-0.2091 * CS + 1.1538) * 0.9688$$
$$ExOcc / CS_{900} = ExOcc / CS / (3.820 * CS - 1.802) * 1.525$$
$$ExCly / CS_{900} = 100 * ExCly / CS / (2.808 * CS + 7.249) * 9.043$$
$$ExClyW / CS_{900} = 100 * ExClyW / CS / (-0.851 * CS + 7.047) * 6.439$$
$$ExCly / ExClyW_{900} = ExCly / ExClyW / (0.6276 * CS + 1.0472) * 1.4628$$

| | |
|---|---|
| $nExCly_{900}$ | $= nExCly / (18.21 * CS - 6.400) * 8.74$ |
| $EL / CS_{900}$ | $= EL / CS / (-0.0687 * CS + 0.3138) * 0.2550$ |
| $MW / CS_{900}$ | $= MW / CS / (0.0599 * CS + 0.5887) * 0.6483$ |
| $ML / CS_{900}$ | $= ML / CS / (-0.0754 * CS + 1.3607) * 1.3029$ |
| $dAN / CS_{900}$ | $= dAN / CS / (0.0086 * CS + 0.2887) * 0.2972$ |
| $MGr / CS_{900}$ | $= 100 * MGr / CS / (3.076 * CS + 0.780) * 3.700$ |
| $Fu2L / CS_{900}$ | $= Fu2L / CS / (-0.00578 * CS + 0.14345) * 0.1375$ |
| $IFu2_{900}$ | $= IFu2 / (0.5660 * CS + 1.2430) * 1.7325$ |
| $PoOc / CL_{900}$ | $= PoOc / CL / (-0.0614 * CS + 0.4391) * 0.3849$ |

and for specimens with CS > 0.9 mm

| | |
|---|---|
| $CL / CW_{900}$ | $= CL / CW / (-0.3804 * CS + 1.4026) * 1.0572$ |
| $SL / CS_{900}$ | $= SL / CS / (-0.2498 * CS + 1.1905) * 0.9688$ |
| $ExOcc / CS_{900}$ | $= ExOcc / CS / (5.106 * CS - 2.960) * 1.525$ |
| $ExCly / CS_{900}$ | $= 100 * ExCly / CS / (0.119 * CS + 9.669) * 9.043$ |
| $ExClyW / CS_{900}$ | $= 100 * ExClyW / CS / (-0.617 * CS + 6.836) * 6.439$ |
| $ExCly / ExClyW_{900}$ | $= ExCly / ExClyW / (0.2168 * CS + 1.4169) * 1.4628$ |
| $nExCly_{900}$ | $= nExCly / (15.54 * CS - 3.995) * 8.74$ |
| $EL / CS_{900}$ | $= EL / CS / (-0.0748 * CS + 0.3193) * 0.2550$ |
| $MW / CS_{900}$ | $= MW / CS / (0.0580 * CS + 0.5904) * 0.6483$ |
| $ML / CS_{900}$ | $= ML / CS / (-0.0903 * CS + 1.3741) * 1.3029$ |
| $dAN / CS_{900}$ | $= dAN / CS / (-0.0076 * CS + 0.3034) * 0.2972$ |
| $MGr / CS_{900}$ | $= 100 * MGr / CS / (2.425 * CS + 1.367) * 3.700$ |
| $Fu2L / CS_{900}$ | $= Fu2L / CS / (-0.01478 * CS + 0.15155) * 0.13750$ |
| $IFu2_{900}$ | $= IFu2 / (0.3325 * CS + 1.4531) * 1.7325$ |
| $PoOc / CL_{900}$ | $= PoOc / CL / (-0.0229 * CS + 0.4047) * 0.3849$ |

These RAV-corrected variables were used in the exploratory and hypothesis-driven data analyses.

**Morphology: Explorative and supervised data analyses, classification and statistical testing**

The formation of species hypotheses was done by an interaction of exploratory data analyses (EDA) and a controlling linear discriminant analysis (LDA). The EDAs applied consisted of three variants of Nest Centroid Custering (NC-Clustering) and of principal component analysis (PCA). NC-clustering was run as hierarchical NC-Ward clustering, non-hierarchical NC-part.means clustering and NC-NMDS.kmeans clustering. These methods were described in more detail by Seifert *et al.* (2014) and Csősz & Fisher (2016). NC-clustering will usually expose species hypotheses more clearly than a PCA but it is also more prone to distortion. The main weakness of NC-clustering is that hybrid samples are usually not exposed as separate cluster, even if making up much of the material, because many of them are absorbed by the clusters of either parental species (Seifert 2021). Similarly, rare species, represented by very few samples in the material, can be swallowed by the cluster of an abundant similar species. A sample-by-sample supervision in the simple vectorial space is needed here to avoid misleading indications. The less sensitive but more robust PCA, which operates in the simple vectorial space, provides a higher probability of exposing intermediate hybrid clusters and to spatially separate single samples of rare species from main clusters. For these reasons a PCA was always run in parallel to NC-clustering and in some cases preferred for hypothesis formation. Removal of allometric variance strongly improves the performance of the PCA but has no effect in the LDA.

Establishment of final species hypothesis was done by the controlling LDA in which samples with classifications disagreeing between NC-clustering methods were run as wild-cards. Nest sample means of posterior probabilities for *n* considered species were obtained by firstly calculating the geometric means $P_1$, $P_2$...$P_n$ of the individual data. The posterior probability for species 1 is then given in the nest-sample mean as $p_1 = P_1 / (P_1 + P_2 ... + P_n)$ and for the other species accordingly. The final classification ("final species hypothesis") was established by the LDA

in the iterative procedure described by Seifert *et al.* (2014). Decisions if morphologically defined clusters can be considered as valid species were achieved according to the GAGE Species Concept which proposed, in an implementing provision, that the mean error of the applied exploratory data analyses determined by the controlling LDA should be < 5%. This threshold proposal appeared reasonable to mitigate taxonomic splitting tendencies. PCA, LDA, and ANOVA tests were performed with the software package SPSS 15.0.

## Genetics

We used nuclear repetitive DNA markers (i.e. microsatellite sequences) to independantly validate morphological species hypotheses. Within a total of more than 1526 sequenced samples, both NUMOBAT and genetic data were available in 274 samples. The latter divide into *Tapinoma nigerrimum* (12 samples), *magnum* (48), *ibericum* (28), *darioi* (29), *hispanicum* **n. sp.** (12), *simrothi* (16), *insularis* **n. sp.** (13), *madeirense* (25) and *subboreale* (77). Molecular and genotyping methods were identical to Centanni *et al.* (2022) and a majority of samples used in the present work were analyzed in that same study. Centanni *et al.* (2022) used the genotypes of morphologically identified samples from Seifert *et al.* (2017) to identify additional genotypes through PCA, Bayesian clustering (e.g. in Cordonnier *et al.* 2019) and maximum-likelyhood assignment. The logic of the present study inverts that of previous works which were not taxonomical in nature but aimed at efficiently identifying large numbers of individuals for ecological and population genetics studies. The objective here was to provide additional characters for taxonomical analysis. Microsatellite markers are neutral, fast-evolving short nuclear regions characterized by size polymorphism that have been extensively used to study population structuring in numerous animal and plant taxa. In ants, a small number of studies have used microsatellites to test species hypotheses alongside with morphology and mtDNA sequencing (e.g., Knaden *et al.* 2005, Eyer *et al.* 2017, Eyer & Hefetz 2018, Seifert *et al.* 2018, Orou *et al.* 2023).

The rationale for microsatellite taxonomy has been summarized in Wham & Lajeunesse, (2016). It is based on allele identity, allele size differences or allele frequencies. Orou *et al.* (2023) and Schultze *et al.* (2019) have used clustering methods, which consider identity and frequencies but not size differences, to obtain groups of individuals that can be compared to clustering by other data types. Wham & Lajeunesse (2016) also used allele sizes through Bruvo distances; this is based on the hypothesis that microsatellite sequences randomly evolve to different size classes in different species. While representing a valid idea for testing species delimitation, size differentiation is not immune to homoplasy or population size effects which would see larger populations (i.e. species with broader distributions or higher densities) feature broader allele size ranges than smaller populations. Here we chose not to use clustering methods or Bruvo distances, which can both be misleading when samples sizes and effective populations sizes differ strongly between inferred species (Puechmaille 2016), which is the case here. We therefore used a genetic PCA method (implemented in the *adegenet* package for the R program, Jombart *et al.* 2008), which does not rely on allele sizes or frequencies. PCA was applied to NUMOBATed individuals of each group of related species, as well as individuals from a broader distribution which were not NUMOBATed. Only one individual per colony was used to avoid bias. PCA loadings were subsequently used for analysis, with details presented in species treatment below.

While PCA can detect hybridization, clustering methods can both detect hybrid and measure hybridization (e.g. Cordonnier *et al.* 2019b), especially if sample sizes between parental species are well-balanced. To test for hybridization between *T. subboreale* and *T. madeirense*, we therefore used Bayesian clustering as implemented in Structure (at K=2, 10 replicate runs with 100,000 burn-in followed by 100,000 test simulations, Pritchard *et al.*, 2000), and used Clumpak to group multiple structure runs (Kopelman *et al.*, 2015). To represent hybridization, we used membership or Q values in the 2 clusters. Individuals with Intermediate values were hypothesized to be hybrids (Fig. 53 and 55).

Genetic tables and graph for each inferred species are given as supplementary material. All ant DNA used for this study is preserved at -20°C at the UCBLZ Zoology Collections of the Université Claude Bernard Lyon 1. Non-used specimens from the same field sites are conserved in 96° ethanol and -20°C at the UBLZ. Researchers interested in using this material for further study should contact B. Kaufmann.

# Results

## Delimitation of species groups

The morphological delimitation of species groups within the genus is problematic. Using morphometry of female castes and considering the structure of male genitalia, the most clearly demarcated group is the *Tapinoma nigerrimum* group composed of T. darioi, *T. hispanicum* **n. sp.**, *T. ibericum*, *T. magnum* and *T. nigerrimum*. A still reasonable grouping is possible with the *Tapinoma simrothi* group which is composed of *T. insularis* **n. sp.**, *T. karavaievi*, *T. phoenicaeum* and *T. simrothi* and the *Tapinoma erraticum* group comprising *T. erraticum*, *T. glabrella* and *T. israelis.* These three groups are confirmed when nest sample means of CS and the 14 fully available RAV-corrected shape and seta characters are run in a LDA. The 288 samples of the *T. nigerrimum* group are completely separated whereas the grouping hypotheses were confirmed in 99.3% of 134 *simrothi* group samples and 97.6% of 124 *erraticum* group samples (Fig. 5). The grouping of the remaining species is more problematic and requires a broad world-wide scope and use of nuclear DNA markers.

The workers of the *T. nigerrimum* group are large-sized and strongly size-polymorphic. The largest major workers of mature colonies have twice the cephalic width (CW) and ninefold the body mass of the smallest minor workers. CW may reach 1385 μm. Species of the *Tapinoma simrothi* complex are also rather size-polymorphic but CW does not exceed 1050 μm—this allows a separation of both species complexes in 20% of the individuals. The length to width ratio of the second funiculus segment is larger in *T. nigerrimum* group workers than in other species including the *T. simrothi* group: $IFu2_{900}$ is frequently 1.72–2.10. The bilateral sum of pubescence hairs and smaller setae protruding at a few microns across margin of clypeal excision is also larger than in other species: $nExCly_{900}$ is frequently 7–21.

The gynes of the *T. nigerrimum* group are much larger than those of other species. Cephalic width CW in 62 specimens $1371 \pm 59$ [1251, 1530]. Species of the *Tapinoma simrothi* group are next similar in size and show a small size overlap: CW is in 29 specimens $1155 \pm 67$ [998, 1290]. With all measurements in mm, a safe separation of both species groups is given by the discriminant D(4) = 36.74 CW–17.427 CL–28.75 ExCly–235.67 Fu2W–1.045. Gynes of the *T. nigerrimum* group have D(4) > 0 and those of the *T. simrothi* group D(4) <0.

In males of the *T. nigerrimum* group the genitalia show in ventral aspect a very broad basimere and a broad shovel-like harpago (Fig. 6) which easily separates from all other species groups (compare also Figs. 3–7 in Seifert 1984). The members of the *Tapinoma simrothi* group show in ventral aspect a gripper-like harpago (Fig. 7).

As shown above, the morphometric separation of workers of the *T. erraticum* group from the *T. simrothi* group is confirmed in 98.5% of the samples. This grouping is supported by male genital morphology. Males of the *T. erraticum* group show a much smaller harpago which is neither shovel- nor gripper-like, the two terminal endings of subgenital plate are much thicker and the inner ends of the basimeres show a long, sharp process directed caudad which is absent in both the *nigerrimum* and *simrothi* group members (Fig. 8).
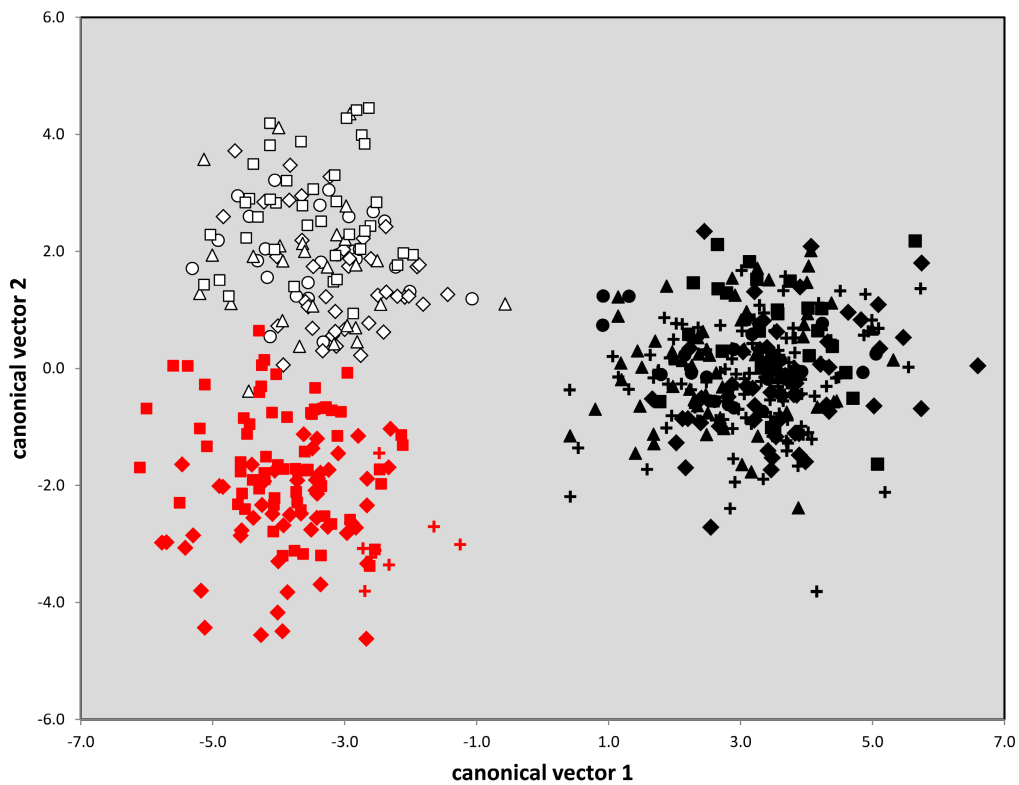
**FIGURE 5.** Separation of 546 sample means of three groups of cryptic species by a linear discriminant analysis considering 15 NUMOBAT characters. Red symbols: *Tapinoma erraticum* group; rhombs *erraticum*, crosses *israelis*, squares *glabrella*. Black symbols: *T. nigerrimum* group; discs *nigerrimum*, squares *hispanicum* **n. sp.**, crosses *magnum*, triangles *ibericum*, rhombs *darioi*. White symbols: *T. simrothi* group; squares *simrothi*, discs *insularis* **n. sp.**, triangles *phoenicaeum*, rhombs *karavajevi*.



**FIGURE 6.** Male genital of *Tapinoma ibericum* in ventral view, Jaen / Spain, 2015.05.

**FIGURE 7.** Male genital of *Tapinoma simrothi* in ventral view, Jamilena / Spain, 2014.04.23.



**FIGURE 8.** Male genital of *Tapinoma erraticum* in ventral view, Balgstädt / Germany, 1991.06.26.

## Key to workers of all species occurring in outdoor habitats of the Palaearctic

This dichotomous key is workable until couplet 9 but this part of the key treated only 38% of the known Palaearctic species. The keying of species groups composed of cryptic species beginning with couplet 10 tried to reduce the number of time-consuming measurements while keeping the error rate reasonably low. Yet, many of the proposed solutions are questionable as they still imply a big workload. Overall, it appears better to numerically record the full set of 15 characters. This takes for the well-equipped, trained and experienced senior author Seifert about 25 minutes per specimen. It is recommended to run then the specimens under investigation as wild-card in a LDA using the data in supplementary information SI1 as reference for determination. Excluded from the key are cosmopolitan tropical tramp species such as *T. melanocephalum* (Fabricius 1793) and *T. pithecorum* Seifert 2022 which only occur in the considered geographical area in greenhouses.

**1a** Extremely small, SL < 475 μm. Clypeal excision absent or extremely shallow, ExCly <8 μm. Mainly Mediterranean zone of West Palaearctic. Figs. 9–11, Tab. 7. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***pygmaeum***

**1b** Larger, SL > 475 μm. Clypeal excision varying from very shallow to deep . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **2**

**2a** Palaearctic eastwards to 60°E. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **7**

**2b** Palaearctic from 60°E to 120°E . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **3**

**3a** Based on image evaluation of two individuals from Tian Shan and Mongolia: Postocular index large, PoOc/CL >0.42. With all measurements in mm, discriminant 64.89*CL -49.21*CW -63.57*PoOc +20.81*SL -8.45 <0. Apparently a small, very short-headed and short-scaped species with shallow clypeal excision, CS 693 and 720 μm, CL/CW 1.016 and 1.053, SL/CS 0.868 and 0.918, ExCly/CS 2.6 and 3.4%. Tian Shan, Mongolia. Figs. 12, 13; Tab. 7 . . . . . . . . . . . . . . . . . . . . . ***sinense***

**3b** Discriminant > 0. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **4**

**4a** Second funiculus segment very short, IFu2 < 1.45. Clypeal excision very shallow and always much wider than deep ExClyL/W <0.66. Discriminant 6.469*IFu2 -1.946*ExClyL/W -11.268 <0. Small species from the montane zone of Sichuan /China . . . **5**

**4b** IFu2 and ExClyL/W larger. Discriminant >0. Unknown from Sichuan. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **6**

**5a** Mesosoma rather thickset, ML/CS <1.335. Dorsal profiles of mesonotum and propodeum more strongly convex, metanotal depression deeper. Figs. 14–16, Tab. 7. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***dabashanica* n.sp.**

**5b** Mesosoma more slender, ML/CS > 1.335. Dorsal profiles of mesonotum and propodeum only feebly convex, metanotal depression shallower. Figs. 17–19, Tab. 7 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***sichuense* n.sp.**

**6a** Margin of clypeal excision forming a sharp cuticular edge beginning from its frontal corners caudad over at least 70% of its length and is in this area at same level as the adjacent clypeal surface It appears as if sharply punched out from a thin plane, plate. Fig.20, right). With all measurements in mm, discriminant 19.06*CW -19.92*CL +70.87*dAN -78.57*EL -0.085*nExCly +50.25*ExCly -110.38*ExOcc +113.82*Fu2L -110.03*Fu2W -16.97*MW + 3.184 < 0 [error 2.4% in 209 individuals, 0% in 67 nest sample means] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***glabrella***

**6b** Edge of clypeal excision slightly curving down below the level of adjacent clypeal surface, thus appearing rather blunt. Fig.20, left). Discriminant >0 [error 5.8% in 121 individuals, 0% in 39 nest sample means] . . . . . . . . . . . . . . . . . . . . . . . ***karavaiewi***

**7a** Second funiculus segment very short, Fu2L/CS <10.9%. With all measurements in mm, discriminant 134.18*Fu2L -14.42*CW -1.184 < 0. Very small species, CS <0.65 mm, clypeal excision very shallow, ExCly/CS <3.5%. S Ukraine and S of European Russia. Figs. 21–23, Tab. 7. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***kinburni***

**7b** Fu2L/CS >10.9%. Discriminant >0. CS frequently >0.65 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **8**

**8a** With all measurements in mm, discriminant 20.29*CL-101.78*dAN+23.03*ExCly+81.31*Fu2L-0.728 < 0. Head very short and with notably excavated posterior margin, mean CL/CW 1.035, ExOcc/CS 1.5%. Clypeal excision very shallow, mean ExCly/CS 3.75%. Distance of antennal socket rings large, dAN/CS 0.322. Only known from Greece and Turkey. Figs. 24–26 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***festae***

**8b** Discriminant > 0. Character combination strongly deviating . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **9**

**9a** Second funiculus segment more elongated, IFu2 1.912 ± 0.102. Clypeal excision with many pubescence hairs or small setae surpassing the upper margin of clypeal excision (Figs 1, 29), nExCly 16.2 ± 6.3. Usually large and very size-polymorphic, CW 0.938 ± 0.179 mm. With all metric data in mm, discriminant 0.119*nExCly -11.4*CL +11.11*CW +35.02*dAN +8.62*EL -28.01*ExCly +3.85*SL +32.35*ExClyW +19.79*ExOcc +135.45*Fu2L -253.50*Fu2W -12.60*MGr -10.54*ML-12.98*MW +6.15 > 0 [error 0.7% in 966 individuals]. *T. nigerrimum* group. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **10**

**9b** Second funiculus segment less elongated, IFu2 1.606 ± 0.107. Clypeal excision with fewer pubescence hairs or small setae surpassing the upper margin of clypeal excision, nExCly 4.8 ± 3.5. Smaller and less size-polymorphic, CW 0.757 ± 0.115 mm, specimens with CW >1.05 mm extremely rare. Discriminant < 0 [error 0.7% in 960 individuals] . . . . . . . . . . . . . . . . . . . . **14**

**10a** With all metric data in mm, discriminant -29.5*CW +51.53*dAN +26.6*EL -51.05*ExCly +25.1*ExClyW -29.98*ExOcc +56.41*Fu2L +141.54*Fu2W +63.37*MGR -10.1 > 0 [error 4.7% in 384 individuals]. Largely West and Central Mediterranean but introduced to Central and W Europe and Azerbaijan. Supercolonial. Tab. 3. . . . . . . . . . . . . . . . . . . . . . . . . . ***magnum***

**10b** Discriminant < 0 [error 2.1% in 582 individuals] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **11**

**11a** With all metric data in mm, discriminant 19.04*CL +57.56*dAN -108.18*EL +22.02*ExCly +35.61*ExClyW +26.49*ExOcc -55.39*Fu2L +158.80*Fu2W+22.53*MGr-18.71*ML-12.96*MW +10.40 > 0 [error 0.6% in 161 individuals]. S France and Spain. Not anthropogenously spread. Usually monodomous colonies . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **12**

**11b** Discriminant < 0 [error 0.7% in 421 individuals]. Largely West and Central Mediterranean but introduced to Central and NW Europe. Supercolonial . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **13**

**12a** With all metric data in mm, discriminant 47.25*SL -27.067*CW -28.67*ExCly -0.067*nExCly +87.18*MGr -14.728 > 0 [error 9.6% in 73 individuals, 21 nest-sample means fully separable with D > 0.15]. S France and N Spain. Tab. 3. . . . . ***nigerrimum***

**12b** Discriminant < 0 [error 4.5% in 88 individuals, 27 nest sample means fully separable with D < 0.15]. Central and S Spain. Figs 27–29, Tab. 3 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***hispanicum*** **n.sp.**

**13a** With all metric data in mm, discriminant 19.44*CL -113.55*dAN +45.86*ExCly +21.53*SL -39.59*ExOcc -150.05*Fu2L+379.6*Fu2W +21.17*MGr -16.89 < 0 [error 6.2% in 210 individuals and 1.6% in 61 nest sample means]. Tab. 3 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***darioi***

**13b** Discriminant > 0 [error 8.5% in 211 individuals and 1.5% in 63 nest sample means]. Tab. 3 . . . . . . . . . . . . . . . . . . . . ***ibericum***

**14a** Clypeal excision very shallow and wider than deep, ExCly/CS 4.98 ± 0.67%, ExClyL/W 0.726 ± 0.087. With all metric data in mm, discriminant 54.85*Excly -28.27*dAN -0.04*nExCly -16.46*SL -41.23*ExClyW +38.87*ExOcc +173.50*Fu2L -44.53*Fu2W -4.94*MW + 5.144 < 0 [error 1.2% in 168 individuals] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **15**

**14b** Clypeal excision deeper and at least as deep as wide, ExCly/CS 10.09 ± 1.97%, ExClyL/W 1.752 ± 0.456. Discriminant > 0 [error 3.1% in 782 individuals] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **16**

**15a** Workers almost inseparable. Males separable by genital morphology: with all data in mm, discriminant 15.35*SPExc +10.52*SPdT -30.12*dSPST -5.22 < 0 [error 0% in 25 specimens]. Figs. 30–33, Tabs. 2, 6 . . . . . . . . . . . . . . . . . ***madeirense***

**15b** Workers almost inseparable. Males separable by genital morphology: discriminant > 0 [error 1.3% in 77 specimens]. Fig. 34, Tabs. 2, 6. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***subboreale***

**16a** Margin of clypeal excision forming a sharp cuticular edge beginning from its frontal corners caudad over at least 70% of its length and is in this area at same level as the adjacent clypeal surface. It appears as if sharply punched out from a thin plane plate (Fig.20, right). With all metric data in mm, discriminant 17.96*CL +74.89*dAN -58.54*EL +72.71*ExCly -15.85*SL -30.07*ExClyW -48.23*ExOcc +43.34*Fu2L -6.606*ML -19.41*MW -0.265 < 0 [error 4.3% in 369 individuals and 0% in 124 nest sample means]. *T. erraticum* group . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **17**

**16b** Edge of clypeal excision slightly curveing down below the level of adjacent clypeal surface, thus appearing rather blunt (Fig.20, left). Discriminant > 0 [error 5.1% in 414 individuals and 0.8% in 134 nest sample means]**.** *T. simrothi* group . . . . . . . . . . . **19**

**17a** Depth of clypeal excision larger, ExCly/CS 8.82 ± 1.35%. Minimum distance of the inner margins of antennal socket rings smaller, dAN/CS 0.286 ± 0.008. With all metric data in mm, discriminant 18.61*CL -37.88*CW +72.70*dAN +43.16*EL -84.94*ExCly +0.111*nExCly +58.18*MGr -10.30 <0 [error 5.9% in 340 individuals and 1.7% in 116 nest sample means] . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **18**

**17b** Depth of clypeal excision lower, ExCly/CS 5.90 ± 0.66%. Minimum distance of the inner margins of antennal socket rings larger, dAN/CS 0.301 ± 0.005. Discriminant > 0 [error 0% in 29 individuals and 0% in 8 nest sample means]. South Turkey to South Israel. Tab. 2. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***israelis***

**18a** Second funiculus segment and scape longer, Fu2L/CS 14.28 ±0.40%, SL/CS 1.017 ±0.022. Eye shorter, EL/CS 0.260 ± 0.007. With all metric data in mm, discriminant 47.8*CL +121.79*EL -21.92*SL -39.55*ExClyW -187.68*Fu2L -11.68*ML -13.5*MW +0.16*nExCly -6.69 <0 [error 0.8% in 131 individuals]. Europe east to 24°E. Figs 35–37, Tab. 2 . . . . . ***erraticum***

**18b** Second funiculus segment and scape shorter, Fu2L/CS 13.41 ±0.40%, SL/CS 0.987 ±0.025. Eye longer, EL/CS 0.271 ± 0.009. Discriminant > 0 [error 0.5% in 209 individuals]. Palaearctic from 11.3°E to 82.3°E. Fig. 20, right; Tab. 2 . . . . . . . . . ***glabrella***

**19a** With all metric data in mm, discriminant 0.045*nExCly+63.44*PoOc -35.80*dAN +64.72*EL +68.58*ExCly -30.02*SL -23.56*ExClyW +94.64*ExOcc -33.70*Fu2L -96.79*Fu2W -28.09*MGr +2.305 > 0 [error 3.9% in 205 individuals and 0 % in 66 nest sample means]. Mediterranean region from 10° W to 16°E but occasionally introduced farther east . . . . . . . . . . . . **20**

**19b** Discriminant < 0 [error 4.3% in 208 individuals and 1.5% in 68 nest sample means]. South Palaearctic from 33°E to 73°E . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **21**

**21a** With all metric data in mm, discriminant 17.82*CW -30.01*CL -82.78*dAN +86.78*ExCly +35.53*SL +64.0*ExClyW -125.50*Fu2W +1.36 < 0 [error 6.0% in 84 individuals and 0 % in 26 nest sample means]. Mediterranean zone between 9 and 16°E, few introductions outside this area. Figs. 38–40, Tab. 5 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***insularis*** **n.sp.**

**20b** Discriminant > 0 [error 7.4% in 121 individuals and 0 % in 40 nest sample means]. Mediterranean zone between 10°W and 10°E. Tab. 5 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***simrothi***

**20a** With all metric data in mm, discriminant 0.111*nExCly -77.37*CL +75.45*PoOc +56.02*dAN+117.44*EL +30.22*SL +83.70* ExClyW -70.58*ExOcc -140.86*Fu2L -214.17*Fu2W +79.04*MGr +13.60*MW -3.077 <0 [error 5.7% in 87 individuals and 0% in 28 nest sample means]. Tab. 5 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***phoenicaeum***

**21b** Discriminant > 0 [error 4.1% in 121 individuals and 0% in 39 nest sample means]. Tab. 5 . . . . . . . . . . . . . . . . . . . . . ***karavajevi***

**FIGURE 9.** *Tapinoma pygmaeum*, head in full face view, Ollon / Switzerland, 2017.05.21.



**FIGURE 10.** *Tapinoma pygmaeum*, lateral view, Eekloo / Belgium, 2022.02.04.

**FIGURE 11.** *Tapinoma pygmaeum*, anterior head in dorsofronal view, Ollon / Switzerland, 2017.05.21.



**FIGURE 12.** *Tapinoma sinense*, type, head in dorsal view, Burgaltai / Mongolia, 1898.09.05; from www.antweb.org, photo Z. Lieberman.

**FIGURE 13.** *Tapinoma sinense* (type of *T. emeryanum* **syn. nov.**), lateral view, Ak Tash / Uzbekistan, from www.antweb.org, photo Z. Lieberman.



**FIGURE 14.** *Tapinoma dabashanica* **n. sp.**, holotype, head in full face view, Gaoguan / China, 2010.05.18.

**FIGURE 15.** *Tapinoma dabashanica* **n. sp.**, holotype, lateral view, Gaoguan / China, 2010.05.18.



**FIGURE 16.** *Tapinoma dabashanica* **n. sp.**, , holotype, anterior head in dorsofronal view, Gaoguan / China, 2010.05.18.

**FIGURE 17.** *Tapinoma sichuense* **n. sp.**, holotype, head in full face view, Jiuxiangzhen /China, 2009.07.08.



**FIGURE 18.** *Tapinoma sichuense* **n. sp.**, holotype, lateral view, Jiuxiangzhen /China, 2009.07.08.

**FIGURE 19.** *Tapinoma sichuense* **n. sp.**, holotype, anterior head in dorsofronal view, Jiuxiangzhen /China, 2009.07.08.
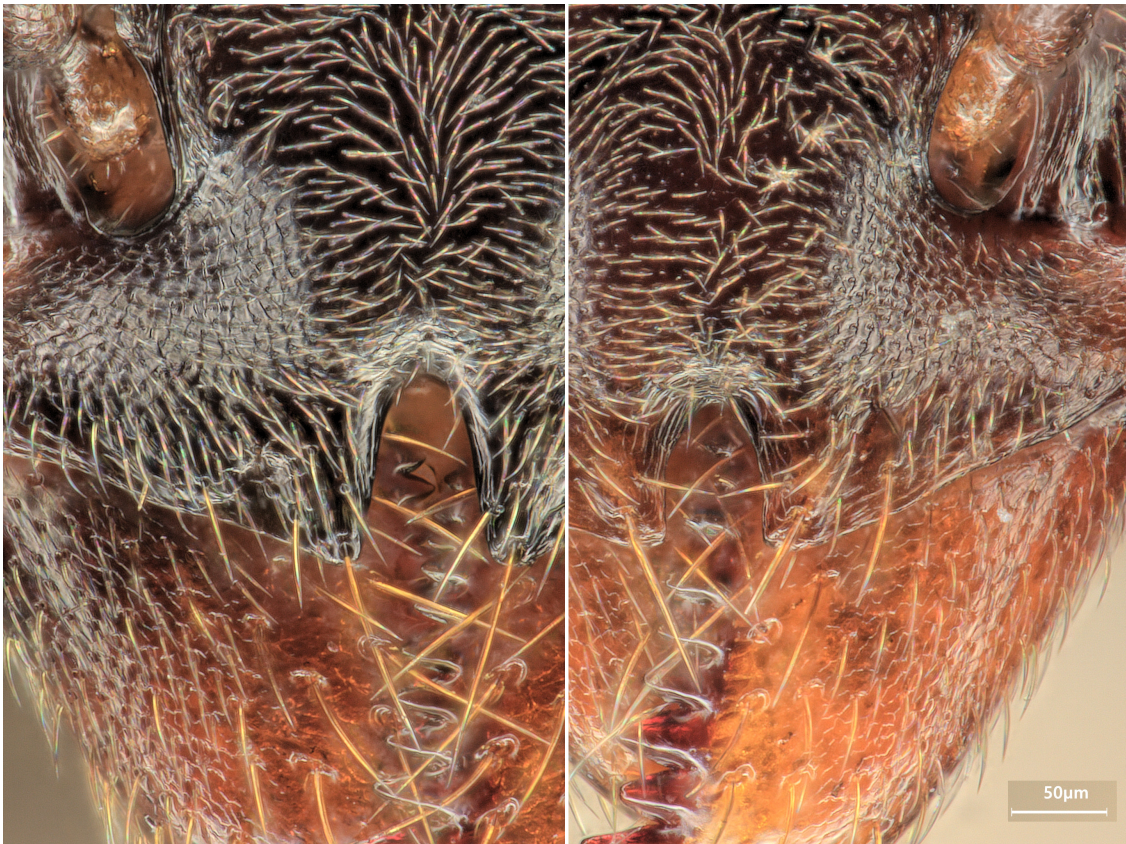


**FIGURE 20.** Clypeal excision of *Tapinoma karavajevi* (left) and *T. glabrella* (right); the broad white reflexion in the left picture indicates the blunt margin of clypeal excision.

**FIGURE 21.** *Tapinoma kinburni*, head in full face view, Rybalche / Ukraine, 1982.06.08.



**FIGURE 22.** *Tapinoma kinburni*, lateral view, Rybalche / Ukraine, 1982.06.08.
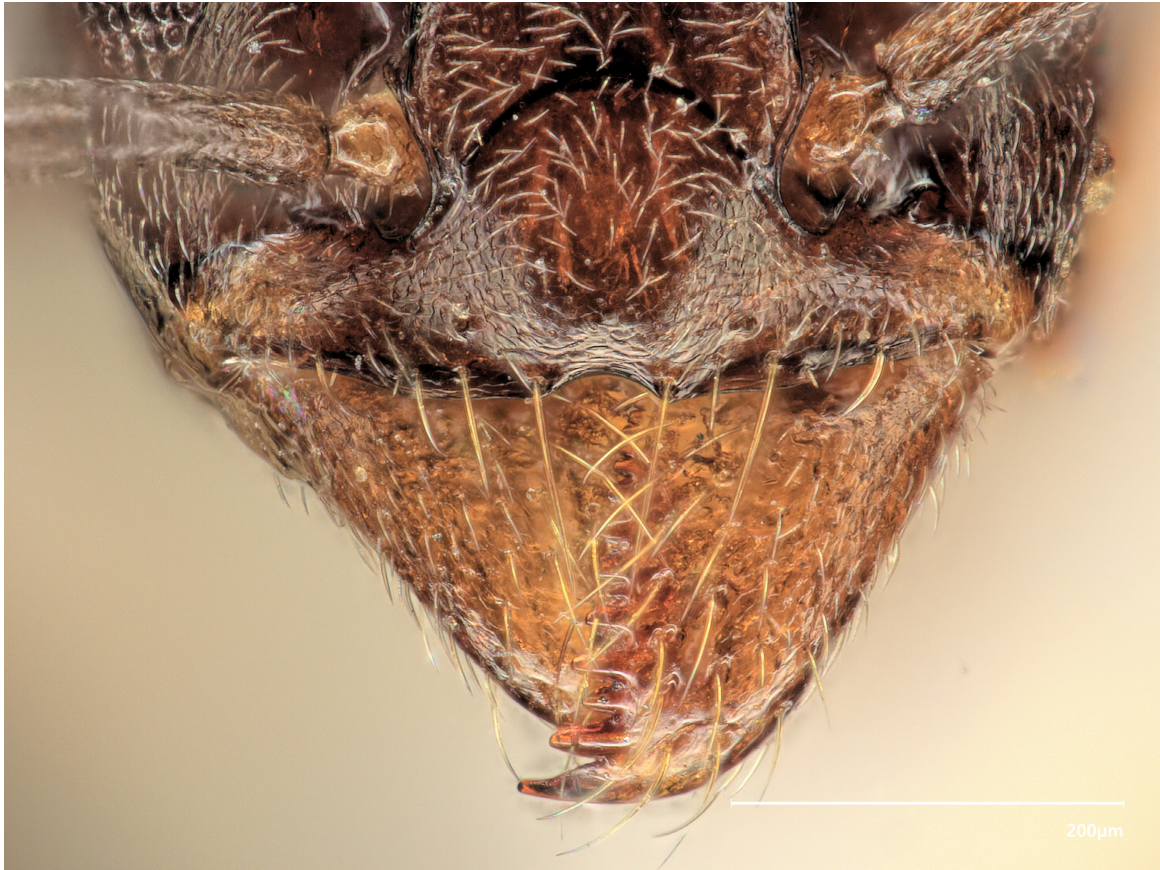
**FIGURE 23.** *Tapinoma kinburni*, anterior head in dorsofronal view, Rybalche / Ukraine, 1982.06.08.



**FIGURE 24.** *Tapinoma festae*, head in full face view, Izmir-Konak / Turkey, 2013.05.17.

**FIGURE 25.** *Tapinoma festae*, lateral view, Izmir-Konak / Turkey, 2013.05.17.



**FIGURE 26.** *Tapinoma festae*, anterior head in dorsofronal view, Izmir-Konak / Turkey, 2013.05.17.

**FIGURE 27.** *Tapinoma hispanicum* **n. sp.**, holotype, head in full face view, Prado del Rey / Spain, 2021.10.20.



**FIGURE 28.** *Tapinoma hispanicum* **n. sp.**, holotype, lateral view, Prado del Rey / Spain, 2021.10.20.

**FIGURE 29.** *Tapinoma hispanicum* **n. sp.**, holotype, anterior head in dorsofronal view, Prado del Rey / Spain, 2021.10.20.



**FIGURE 30.** *Tapinoma madeirense*, head in full face view, Belem / Portugal, 2018.03.25.

**FIGURE 31.** *Tapinoma madeirense*, lateral view, Belem / Portugal, 2018.03.25.



**FIGURE 32.** *Tapinoma madeirense*, anterior head in dorsofronal view, Belem / Portugal, 2018.03.25.

**FIGURE 33.** *Tapinoma madeirense*, male genital in ventral view, Meio da Serra / Madeira, 2002.06.22.



**FIGURE 34.** *Tapinoma subboreale*, male genital in ventral view, Percile / Italy, 2013.06.23.

**FIGURE 35.** *Tapinoma erraticum*, neotype, head in full face view, Nespouls-Faugère / France, 2008.07.02.



**FIGURE 36.** *Tapinoma erraticum*, neotype, lateral view, Nespouls-Faugère / France, 2008.07.02.

**FIGURE 37.** *Tapinoma erraticum*, neotype, anterior head in dorsofronal view, Nespouls-Faugère / France, 2008.07.02.



**FIGURE 38.** *Tapinoma insularis* **n. sp.**, holotype, head in full face view, Portopalo / Italy, 2013.04.02.

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**FIGURE 39.** *Tapinoma insularis* **n. sp.**, holotype, lateral view, Portopalo / Italy, 2013.04.02.



**FIGURE 40.** *Tapinoma insularis* **n. sp.**, holotype, anterior head in dorsofronal view, Portopalo / Italy, 2013.04.02.

**Taxonomic treatment by species**

The main sources for identification of a taxon are given in square brackets after taxonomic name, author and year.

### *Tapinoma erraticum* (Latreille 1798)

*Formica erratica* Latreille 1798 [type investigation]
The species has been described from Brive, France . Investigated were the neotype worker plus two workers from the neotype nest labelled "FRA: 45.0517°N, 1.5372°E, Nespouls-Faugère, 330 m, along road, under stone, leg. Galkowski 2008.07.02" and "Neotype *Tapinoma erraticum* (Latreille 1798), design. B.Seifert 2010"; depository SMN Görlitz. The neotype sample is allocated to the *T. erraticum* cluster with p=1.000 in a wild-card run of a LDA considering 12 morphometric characters (see below).

*Tapinoma collina* Foerster 1850 [zoogeography and original description]
The species has been described from near Königswinter and Boppard / Germany (" Siebengebirge und bei Boppard auf Bergwiesen"). Types are obviously lost. According to zoogeography and the situation in the 19th century without invasive species present, only two species may have occurred in the terra typica: *T. erraticum* and *T. subboreale.* As Foerster (1850, p. 43–44) described the anteromedian clypeus in both workers and gynes to be deeply and almost circularly excavated ("Clypeus in der Mitte tief und fast rundlich ausgeschnitten"), a conclusion on junior synonymy with *T. erraticum* is reasonable—at least, due to the abscence of types, no counterevidence can be given. Alternatively this taxon could be placed under Incertae Sedis.

*Tapinoma erraticum platyops* Emery 1925 [type investigation]
The type series was collected in Vaux near Morges / Switzerland. Investigated were two worker syntypes labelled "T. erraticum var. platyops Emery" [Emery's handwriting], "Morges Vaux Forel € e c. y" [Forel's handwriting], "ANTWEB CASENT 0904023", "SYNTYPUS Tapinoma erraticum platyops Emery, 1925"; 1 syntype male labelled "20. VI. Forel § "; depository all MCSN Genova. The syntype sample is allocated to the *T. erraticum* cluster with p=0.9992 in a wild-card run of a LDA considering 12 morphometric characters (Tab. 1).

*Tapinoma erraticum bononiensis* Emery, 1925 [type investigation]
The species has been described from the vicinity of Bologna / Italy. Investigated were the lectotype worker and 2 paralectotype workers labelled "Bologna" [Emery's handwriting], "Lectotype Tapinoma erraticum bononiensis Emery, 1925 bottom specimen des. B.Seifert 2013"; depository MCSN Genova. The lectotype series is allocated to the *T. erraticum* cluster with p=0.9292 in a wild-card run of a LDA considering 12 morphometric characters (Tab. 1).

**Material examined**. Numeric phenotypical data were taken in 49 worker samples (largely nest samples) with 131 workers. They originated from Bosnia (1 sample), Bulgaria (1), Czechia (2), France (5), Great Britain (1), Germany (19), Greece (1), Italy (14), Macedonia (1), Serbia (1), Slovenia (1), Spain (1) and Switzerland (1). For details see supplementary information SI1, SI2.

**Geographic range**. European, south temperate and submeridional. According to examined vouchers the range includes S England, N Spain, France, Central Europe north to 52°N, Italy and the West Balkans. The eastern and southern limits of the range are marked by 24° E and 39°N.

Ascending to 950 m in Baden-Württemberg, to 1300 m on highly montane pastures of Vorarlberg and to 1800 m in the Pyrenees (42.7°N).

**Diagnosis**:—Worker (Tab. 2, Figs. 35–37): All shape ratios given below are, in contrast to those in Tab. 2, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Medium sized to small, CS 763 ± 88 μm. Head moderately elongated CL/CW 1.123 ± 0.043. Postocular distance medium-sized, PoOc/CL 0.409 ± 0.009. Anteromedian clypeal excision usually deeper than wide, ExCly/CS 8.42 ± 0.87 %, ExClyW 6.58 ±

0.65 %. The margin of clypeal excision forms a sharp cuticular edge beginning from its frontal corners caudad over at least 70% of its length and is in this area at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few microns across margin of clypeal excision low, nExCly $2.57 \pm 1.53$. Posterior margin of head in full face view in medium-sized and large specimens slightly excavated, ExOcc/CS $1.35 \pm 0.63$ %. Scape moderately elongated, SL/CS $1.017 \pm 0.022$. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN/CS $0.289 \pm 0.008$. Eye medium-sized, EL/CS $0.260 \pm 0.007$. Metanotal groove rather deep, MGr/CS $3.87 \pm 0.91$ %. Mesosoma relatively wide and long, MW/CS $0.665 \pm 0.025$, ML/CS $1.355 \pm 0.029$. Second funiculus segment moderately long and slender, Fu2L/CS $14.29 \pm 0.40$ %, IFu2 $1.634 \pm 0.071$. Head, mesosoma and gaster covered by a rather dense pubescence. Anterior margin of clypeus with a few standing setae, the two longest and strongest are based near to the anterolateral margin of clypeal excision. Remaining surface of head capsule and dorsal mesosoma without standing setae, such are present on mandibles, coxae and ventral surface of gaster. Head, mesosoma and gaster dark blackish brown. Antennae, femora and tibia dark brown. Tarsae and metatarsae usually pale yellowish brown.

—Male genital (Fig. 08): Ventral aspect. Lobes of subgenital plate rather broad, their length extends over 60 to 80% of the visible length of the basimere. Apical margins of the lobes straight to weakly convex. The mediodistal part of the basimere forms a sharp spine-like extension directed caudad. Harpago segments rather small, their lateral margins are only weakly incurved towards the tip.

**Taxonomic comments.** Based on worker morphology, the next relatives of *Tapinoma erraticum* are *T. israelis* and *T. glabrella*. The 128 nest samples of these three species can be fully separated by a principal component analysis using the RAV-corrected characters CL/CW$_{900}$, SL/CS$_{900}$, ExCly/CS$_{900}$, ExClyW/CS$_{900}$, ExClyL/W$_{900}$, nExCly$_{900}$, dAN/CS$_{900}$, EL/CS$_{900}$, MGr/CS$_{900}$, MW/CS$_{900}$, ML/CS$_{900}$, and Fu2L/CS$_{900}$ (Fig. 41). Using the same characters, 96.3% of 380 worker individuals are correctly classified by linear discriminant analysis (LDA) and the nest sample means form widely separate clusters. The classification of the type series of the species related to *T. erraticum* according to wild-card runs of the LDA is given in Tab. 1. A relatedness of *T. erraticum* and *T. glabrella* is indicated by the similarity of the basic structure of male genitalia. The male of *T. israelis* is unknown.

**Biology:** For a condensed description of biology see Seifert (2018) but see also Wagner (2019) and De Pletincx & Aron (2022).

**TABLE 1.** Posterior probabilities of type series of taxa related to *Tapinoma erraticum* in wild-card runs of a LDA considering 12 RAV-corrected characters.

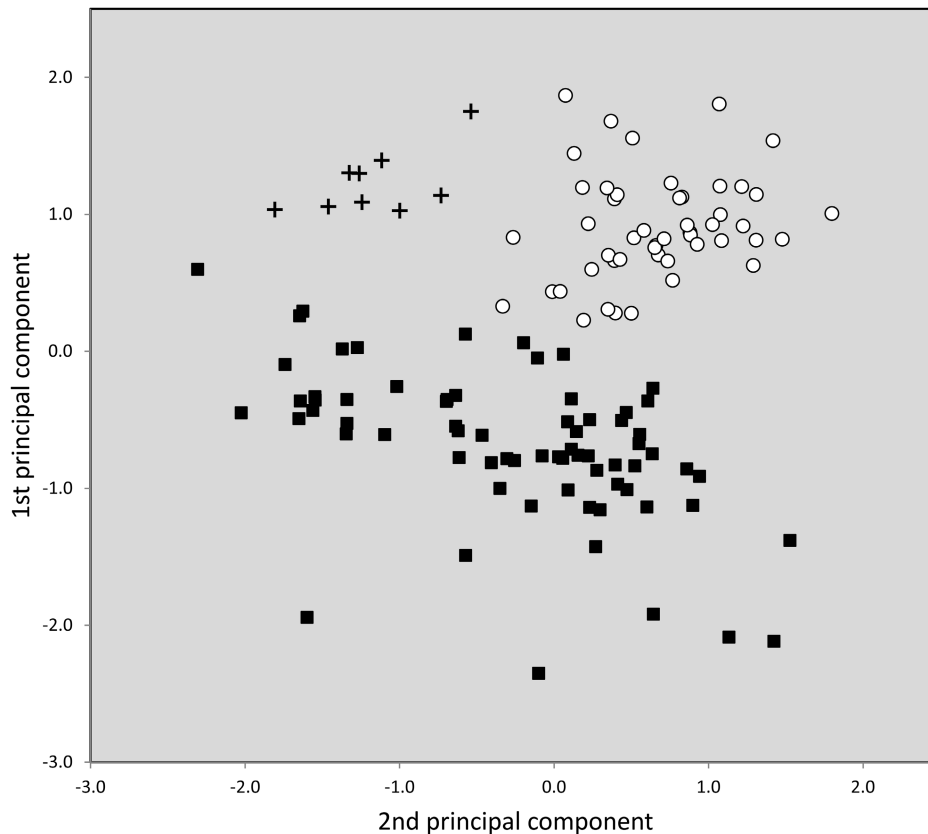| | p (*erraticum*) | p (*glabrella*) | p (*israelis*) |
|---|---|---|---|
| Neotype sample *T. erraticum* (Latreille 1798) | 1.0000 | 0.0000 | 0.0000 |
| Syntypes *T. platyops* Emery 1925 | 0.9992 | 0.0002 | 0.0006 |
| Lectotype sample *T. bononiensis* Emery 1925 | 0.9292 | 0.0364 | 0.0345 |
| Lectotype *T. glabrella* (Nylander 1849) | 0.0000 | 0.9998 | 0.0002 |
| Syntype sample *T. breve* Emery 1925 | 0.0002 | 0.9446 | 0.0552 |
| Paratype worker *T. tauridis* Emery 1925 | 0.0002 | 0.9960 | 0.0039 |
| Syntype sample *T. israelis* Forel 1904 | 0.0059 | 0.0017 | 0.9924 |

**FIGURE 41.** Nest sample means of the first two principal components extracted from 12 RAV-corrected phenotypical characters. Black squares—*Tapinoma glabrella* (n=70); white dots—*T. erraticum* (n=49); black crosses *T. israelis* (n=9).

## *Tapinoma glabrella* (Nylander 1849)

*Formica glabrella* Nylander 1849 [type investigation]
The species has been described from Cherkassy /Ukraine. Investigated were two type workers on two different pins, both deposited in ZM Helsinki. One worker labelled "Tscherkassk", "Motschoulsky", "Coll. Nyland.", "Motsch. 23", "Spec. type No. 5092 *Formica glabrella* Nyl." was fixed by present designation as lectotype. The type series is allocated to the *T. glabrella* cluster with p=0.9998 in a wild-card run of a LDA considering 12 morphometric characters (Tab. 1). The paratype worker on the other pin had the same labelling except for "Spec. type No. 5093 *Formica glabrella* Nyl.". It belongs to *Tapinoma subboreale* (see there).

*Tapinoma tauridis* Emery 1925, **syn. nov.** [type investigation]
The taxon has been described from the Crimea based on collections made by Mejunov and Karavajev. Investigated were two type specimens, a male and a worker, from MCSN Genova.

The male, labelled "Crimée Mejunoff", "SYNTYPUS Tapinoma tauridis Emery, 1925" was fixed by present designation as lectotype ("Lectotype Tapinoma tauridis Emery 1925, des. B Seifert 2015") . A synonymization with *T. erraticum* and *israelis* is excluded by geographic indication. The syntype worker is labelled "Crimée Karavaiev", "T. tauridis Emery"[Emery's handwriting], "ANTWEB CASENT 0904021", "SYNTYPUS Tapinoma tauridis Emery, 1925". It is allocated to the *T. glabrella* cluster with p=0.9960 in a wild-card run of a LDA considering 12 morphometric characters (Tab. 1).

*Tapinoma breve* Emery 1925, **syn. nov.** [type investigation]

The taxon has been described based on material collected by Kuznetzov-Ugamsky in the Kysyl valley, former Syr Darja province, at an elevation of 6000 feet. According to the altitude record, the site must be in the NW Tian Shan (approximately at 42.5°N, 71.6°E) and belongs to the present Kyrgistan. Investigated were two syntype workers from MCSN Genova, labelled "Prov. Syr Darja, Kisil Tal", "T. breve Emery"[Emery's handwriting], "ANTWEB CASENT0904020", "SYNTYPUS Tapinoma breve Emery, 1925". The specimen CASENT0904020 with CW=644 is fixed by present designation as lectotype. The other type specimen has CW= 563. The type sample is allocated to the *T. glabrella* cluster with p=0.9446 in a wild-card run of a LDA considering 12 morphometric characters (Tab. 1).

**Material examined**. Numeric phenotypical data were taken in 70 samples (largely nest samples) with 219 workers. They originated from Albania (3 samples), Bulgaria (8), Croatia (9), France (1), Georgia (2), Greece (3), Iran (3), Italy (6), Kazakhstan (2), Kyrgistan (17), Montenegro (4), Slovenija (3), Turkey (7) and Ukraine (2). For details see supplementary information SI1, SI2.

**Geographic range**. Widely distributed over the Mediterranean, Submediterranean, Ponto-South-Siberian and Turanian regions of the West and Central Palaearctic. The western, eastern, southern and northern range limits are at 3.9°E in France, at 82.3°E in Kazakhstan, at 33.2°N in Central Iran and at 49.4°N in the Ukraine. Ascending to 2500 m at 38.5°N in Turkey. Broadly sympatric with *T. erraticum* in Italy and the W Balkans and there is a small sympatric zone with *T. israelis* in Asia Minor.

**Diagnosis**:—Worker (Tab. 2): All shape ratios given below are, in contrast to those in Tab. 2, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Slightly larger than *erraticum*, CS 777 ± 83 μm. Head moderately elongated CL/CW 1.124 ± 0.046. Postocular distance medium-sized, PoOc/CL 0.405 ± 0.011. Anteromedian clypeal excision slightly deeper and narrower than in *erraticum*, ExCly/CS 9.07 ± 1.53 %, ExClyW 5.84 ± 0.70 %. The margin of clypeal excision forms a sharp cuticular edge beginning from its frontal corners caudad over at least 70% of its length and is in this area at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few micron across margin of clypeal excision larger than in *erraticum*, nExCly 4.87 ± 3.50. Posterior margin of head in full face view in medium-sized and large specimens slightly excavated, ExOcc/CS 1.17 ± 0.77 %. Scape shorter than in *erraticum*, SL/CS 0.987 ± 0.025. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN/CS 0.285 ± 0.008. Eye slightly larger than in *erraticum*, EL/CS 0.271 ± 0.009. Metanotal groove moderately deep, MGr/CS 3.12 ± 1.03 %. Mesosoma slightly narrower and shorter than in *erraticum*, MW/CS 0.648 ± 0.023, ML/CS 1.324 ± 0.035. Second funiculus segment shorter than in *erraticum*, Fu2L/CS 13.41 ± 0.40 %, IFu2 1.579 ± 0.083. Seta condition, pubescence and pigmentation similar to *T. erraticum*.

—Male genital (Fig. 02): Ventral aspect. In basic structure similar to *erraticum* and showing a lot of variation which prevents a clear species separation by simple eye inspection. Lobes of subgenital plate rather broad, their length extends over 50 to 90% of the visible length of the basimere. The apical margins of the lobes vary from straight to semicircular. The shape of the mediodistal part of the basimere shows various transitions between three extremes: (1) it may form a sharp hook the tip of which is directed mediad, (2) it is straight and directed mediocaudad and shows a rather blunt chisel-like tip, (3) it forms a sharp spine-like extension directed caudad. The harpago segments are rather small, their lateral margins are usually more strongly incurved towards the tip than in *erraticum*.

**Taxonomic comments.** The clear separation of workers from *Tapinoma erraticum* and *T. israelis* was shown in the section on *Tapinoma erraticum*. In contrast to the rather monomorphic situation in *T. erraticum*, the *T. glabrella* worker population shows a high variation due to significant geographic substructuring within its huge range. This is mirrored by the situation in male genitalia. Reasons for the synonymization of *Tapinoma tauridis* Emery 1925 and *Tapinoma breve* Emery 1925 based on investigation of type specimens are given in the explanatory text within the account of synonymies.

**Biology.** Among 27 records with information on habitat, 25 referred to open land and 2 to light broad-leafed forest. Within the open land habitats, pastures and uncultivated dry grasslands dominated but the list included also rural and urban habitats such as road sides, gardens or city parks. Furthermore, it occurred on gravel banks of floodplains, here occasionally in rather moist conditions, and one nest was found in a moving aeolic sand dune. Nests were polygynous and the main period for occurrence of alates was 3 May to 6 June.

### *Tapinoma israelis* Forel 1904

*Tapinoma erraticum* r. *israelis* Forel 1904 [type investigation]

The taxon has been described from Jerusalem / Palestine. Investigated were five syntype workers on two pins labelled "T. israelis type For. Jerusalem", "Type", MNH Genève. The type series is allocated to the *T. israelis* cluster with p=0.9224 in a wild-card run of a LDA considering 12 morphometric characters (Tab. 1).

**Material examined**. Numeric phenotypical data were taken in 9 samples with 30 workers. They originated from Israel (6 samples), Jordan (1) and Turkey (2). For details see supplementary information SI1, SI2.

**Geographic range**. According to the data available only known from five sites in Israel and one site each in Jordan and Asia Minor at elevations from sea level up to 1000 m.

**Diagnosis**:—Worker (Tab.2): All shape ratios given below are, in contrast to those in Tab. 2, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Smaller than *glabrella*, CS 728 ± 67 µm. Head more elongated than in *glabrella* CL/CW 1.172 ± 0.043. Postocular distance medium-sized, PoOc/CL 0.412 ± 0.006. Anteromedian clypeal excision shallower than in *glabrella*, ExCly/CS 5.84 ± 0.71 %, ExClyW 5.74 ± 0.62 %. The margin of clypeal excision forms a sharp cuticular edge beginning from its frontal corners caudad over at least 70% of its length and is in this area at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few micron across margin of clypeal excision lower than in *glabrella*, nExCly 2.08 ± 0.79. Posterior margin of head in full face view in medium-sized and large specimens slightly excavated, ExOcc/CS 0.80 ± 0.46 %. Scape slightly longer than in *glabrella*, SL/CS 1.015 ± 0.019. Minimum distance of the inner margins of antennal socket rings larger than in *glabrella*, dAN/CS 0.300 ± 0.005. Eye medium-sized, EL/CS 0.276 ± 0.005. Metanotal groove deeper than in *glabrella*, MGr/CS 3.94 ± 0.57 %. Mesosoma slightly longer than in *glabrella*, MW/CS 0.641 ± 0.018, ML/CS 1.355 ± 0.026. Second funiculus segment longer than in *glabrella*, Fu2L/CS 14.25 ± 0.34 %, IFu2 1.640 ± 0.066. Seta condition, pubescence and pigmentation similar to *T. erraticum*.

—Male genital: unknown.

**Taxonomic comments.** The clear separation of workers from *Tapinoma erraticum* and *T. glabrella* was shown above.

**Biology.** Unknown. One nest was found under a stone at the border of a conifer forest.

### *Tapinoma nigerrimum* (Nylander 1856)

*Formica nigerrima* Nylander 1856 [type investigation]

The taxon has been described from a dry place near Montpellier, France ("Locus aridis prope Monspelium". Investigated was the neotype worker (fixed by Seifert *et al*. 2016) and additional two workers from the neotype nest, labelled "FRA: 43.6843° N, 3.8763° E, Prades-le-Lez-1.5 SE, 88 m, monodomous colony, Kaufmann 2012.04.30 - K"; depository SMN Görlitz. A wild-card run in a 5-class LDA considering the five morphologically separable entities of the *T. nigerrimum* species complex allocates the neotype sample with p=0.9954 to the *T. nigerrimum* cluster.

**Material examined**. Numeric phenotypical data were taken in 21 samples with 73 workers. They originated from France (18 samples) and Spain (3). For details see supplementary information SI1, SI2.

**Geographic range**. So far only known from ten sites within a 20 000 km² area in S France and the eastern Catalan Pyrenees, delimited by 1.78°E and 5.24°E and 42.33°N and 44.03°N. The altitudinal range extends from sea level up to 1561 m in the Catalan Pyrenees.

**Diagnosis**:—Worker (Tab. 3): All shape ratios given below are, in contrast to those in Tab. 3, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Largest Palaearctic species, CS 1029 ± 193 µm. Head very broad CL/CW 1.004 ± 0.069. Postocular distance rather small and excavation of hind margin of vertex large, PoOc/CL 0.380 ± 0.010, ExOcc 2.99 ± 1.33 %. Anteromedian clypeal excision rather deep and wide, ExCly/CS 9.85 ± 0.89 %, ExClyW 6.70 ± 0.64 %. The posterior, semicircular end of clypeal excision forms a concave plane delimited by a sharp ventral and a less sharp dorsal edge. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge very large, nExCly 16.9 ± 6.4. Scape moderately long, SL/CS 0.929 ± 0.052. Minimum distance of the inner margins of antennal socket rings moderately large, dAN/CS 0.302 ± 0.006. Eye smaller than in the supercolonial related species, EL/CS 0.226 ± 0.016. Metanotal groove deep, MGr/CS 4.09 ± 0.76 %. Mesosoma shorter and narrower than in the supercolonial related species,

ML/CS 1.222 ± 0.032, MW/CS 0.618 ± 0.012. Second funiculus segment shorter than in the supercolonial related species, Fu2L/CS 13.52 ± 0.45 %, IFu2 1.839 ± 0.091. All body parts including appendages covered by a rather dense pubescence. Setae on dorsal and lateral surfaces of head and mesosoma absent. Longe seta are found on hind margin of 3rd and 4th gaster segment, ventral parts of coxae and anterior clypeus. All body parts blackish brown. Mandibles, edge of clypeus and sometimes antennal funiculus and tarsae with an orange or reddish color component.

**Taxonomic comments.** The *T. nigerrimum* group contains five entities separable by NUMOBAT and microsatellite data: the largely monodomous *T. nigerrimum* and *T. hispanicum* **n. sp.** and the supercolonial *T. ibericum*, *T. darioi* and *T. magnum.* Within a total of 129 samples belonging to this group and being both phenotyped and genotyped, the agreement of NUMOBAT and genetic classification was 97.7% which is a really good performance considering the morphological crypsis of the species. Below we describe the run of exploratory and hypothesis-driven data analyses in two blocks.


Block 1: Species hypothesis formation based on NUMOBAT data

This included in the first step of analysis running all five entities in NC-part.kmeans and NC-Ward using CS and 14 RAV-corrected characters (except PoOc/CL$_{900}$ were data were incomplete). Within the 288 nest samples analyzed, the exploratory data analyses revealed three main clusters (Fig.42). The first main cluster (composed of 48 samples of *T. nigerrimum* and *T. hispanicum* **n. sp.**) was demonstrated by the EDAs with 100 % agreement whereas the classification of the second (composed of 124 samples of *T. darioi* and *T. ibericum*) and the third main cluster (composed of 116 samples of *T. magnum*) disagreed in 2.3 % of the samples.

In a second step of analysis the first main cluster, the 48 samples of *T. nigerrimum* and *T. hispanicum* **n. sp.**, were run in NC-Ward, NC-part.kmeans and NC-NMDS.kmeans using all 15 characters (Fig.43). Disagreement between the EDAs was given in a single sample the determination of which was rectified as belonging to *T. nigerrimum* by a wild-card run in a LDA. All nest samples were classified by the LDA with posterior probabilities of p >0.893 and the type series of *T. nigerrimum* and *T. hispanicum* **n. sp.** were allocated in wild-card runs to the corresponding clusters with p = 0.999 and p = 0.998 respectively.

The second and third main cluster—altogether 240 nest samples and composed of the supercolonial species *T. ibericum*, *T. darioi* and *T. magnum*—were analyzed by NC-part.kmeans and NC-Ward. Both EDAs confirmed the existence of three clusters but disagreed in the classification of 8.8% of the samples. The species hypotheses of these unclear samples were then determined by wild-card runs in a LDA using all 15 characters. Relative to the controlling LDA, the misclassification by NC-part.kmeans was 4.9% in *T. darioi*, 3.2% in *T. ibericum* and 5.2% in *T. magnum.* The total disagreement of 4.4% over three entities justifies to hypothesize them as sufficiently divergent morphospecies. These hypotheses are strongly supported by running a 3-class LDA using 12 selected characters (nExCly$_{900}$, ML/CS$_{900}$ and MW/CS$_{900}$ were excluded) resulted in a mean classification error of 6.7% within 778 individuals but a complete separation on the nest sample level (Fig.44).


Block 2: Confirmation of NUMOBAT-based species hypotheses by genetic data

All five species clusters demonstrated by NUMOBAT could be confirmed by nuclear DNA. In a first step the first five principal components of microsatelite data of all 805 samples genotyped and belonging to this group were extracted. Then a LDA was run using these principal components as characters and and imposing the NUMOBAT classifications as hypotheses. Because the smallest class had only 12 samples and in order to avoid overfitting, the LDA used only the first four principal components. This procedure resulted in a very strong separation of *T. nigerrimum* and *T. magnum* and 100% agreement with NUMOBAT classification (Fig.45). On the other hand, this genetic data set completely failed to confirm the very strong NUMOBAT separation of *T. hispanicum* **n. sp.** and *T. ibericum* (Fig. 42) but provided a rather good separation of *T. darioi* from the collective cluster formed by *T. hispanicum* **n. sp.** and *T. ibericum.*

As next step of analysis the clearly separated *T. magnum* and *T. nigerrimum* samples were removed from the data set and the PCA of genetic data was run only with those 69 *T. darioi*, *T. hispanicum* and *T. ibericum* samples where both NUMOBAT and microsatellite data were available. A character-reduced LDA used only the PCA axes 1 and 3 as characters and removed axis 2 from the calculation as the latter only served to separate one individual having

an unusual allele at one locus (Fig. 46). As result, 95.7% of NUMOBAT classifications in the 69 samples were confirmed by genetic data with one disagreement in each class. The posterior probabilities of the three controversial samples as calculated in wild-card runs of an LDA are shown in Tab. 4.

The Malaga sample is from a supercolony on the castle mountain near to the historic centre of Malaga Thus, colony structure and habitat speak against the genetic classification as *T. hispanicum* **n. sp.** The weak allocation to *T. darioi* by NUMOBAT data appears also rather unlikely since the natural range of *T. darioi* does not include S Spain. However, the anthropogenous dispersal capacity of this species should allow a transport to the south. Taking all indications together—zoogeography, colony structure and the combined posterior probabilities of NUMOBAT and genetic data—this sample should represent *T. ibericum* or a hybrid with participation of this species. The genetic classification of the sample from a supercolony in Rotterdam as *T. hispanicum* **n. sp.** is with a high probability wrong because the NUMOBAT signal pointing to *T. ibericum* is strong and because the former has never been introduced to areas outside Spain nor is it known to form supercolonies. The genetic classification of the sample from Lona de los Panaderos as *T. darioi* is also with certainty wrong because there is an extremely strong NUMOBAT indication as *T. hispanicum* **n. sp.** which is strongly supported by ecological indication: The altitude of this site (2300 m a.s.l.) is far above the upper altitudinal limit of any other species of the *T. nigerrimum* group—specifically T. *darioi* has never been found higher than 722 m.

**Biology.** *Tapinoma nigerrimum* frequently shows monodomous, not very large colonies which behave aggressively to each other. Polydomous colonies seem to exist but true supercoloniality or an invasive potential was not observed so far. Furthermore, in contrast to the supercolonial species, there is a trend in *T. nigerrimum* to dominate in semi-natural and rural habitats—without completely avoiding habitats with stronger anthropogenous impact (Centanni *et al.* 2022). The rarity in coastal areas is probably a consequence of competition by the three supercolonial species. Alates were observed: 4 May ± 10 d [29 April–21 May] n = 5.
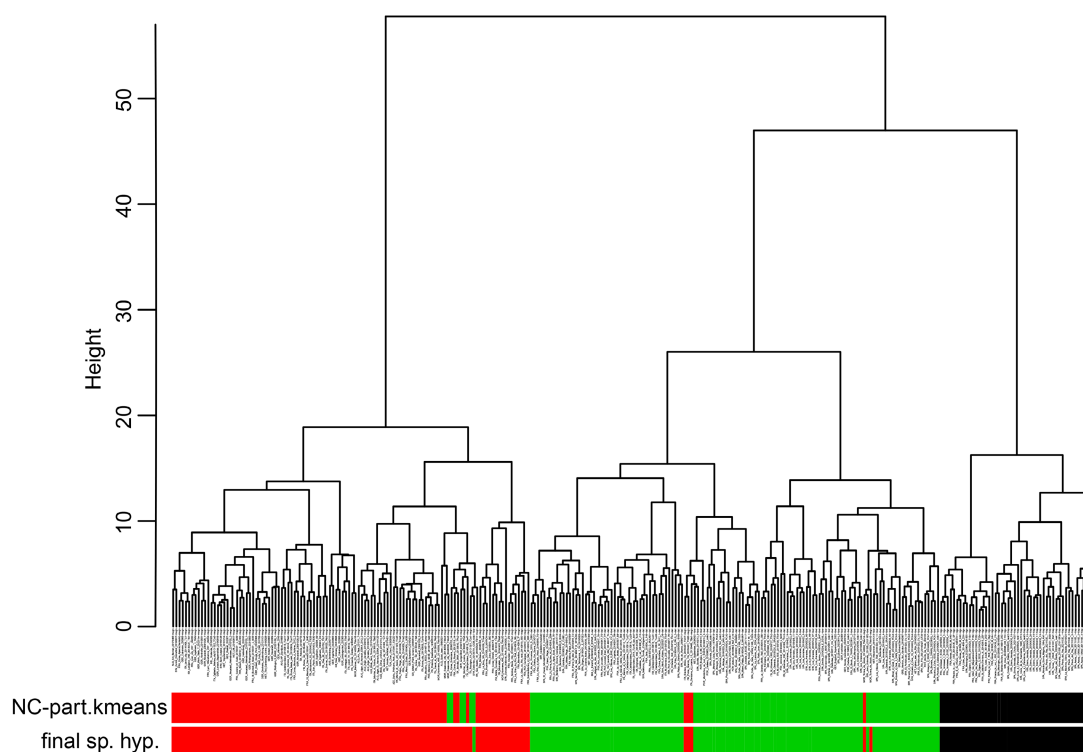


**FIGURE 42.** Demonstration of three main clusters within worker nest samples of the *Tapinoma nigerrimum* group by NC-Ward and NC-part.kmeans clustering considering 15 RAV-corrected phenotypical characters. Red cluster—*T. magnum*; green cluster—*T. darioi* & *T. ibericum*; black cluster—*T. hispanicum* **n. sp.** & *T. nigerrimum*. The classification error of NC-part. kmeans relative to the controlling linear discriminant function is 2.1% for K=3.
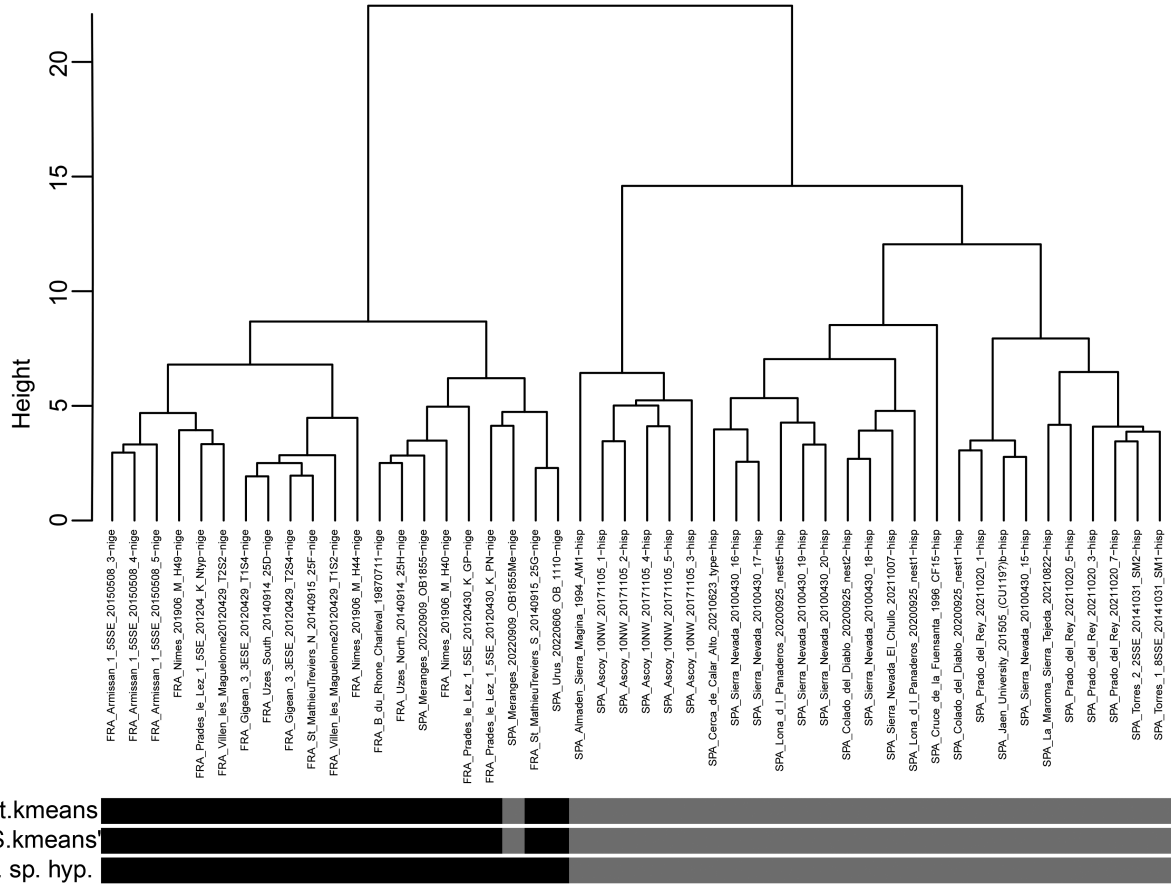
**FIGURE 43.** Separation of worker nest samples of *Tapinoma hispanicum* **n. sp.** (grey bars) and *T. nigerrimum* (black bars) by three methods of NC clustering. The mean error of the three exploratory data analyses relative to the controlling linear discriminant function is 1.4%.
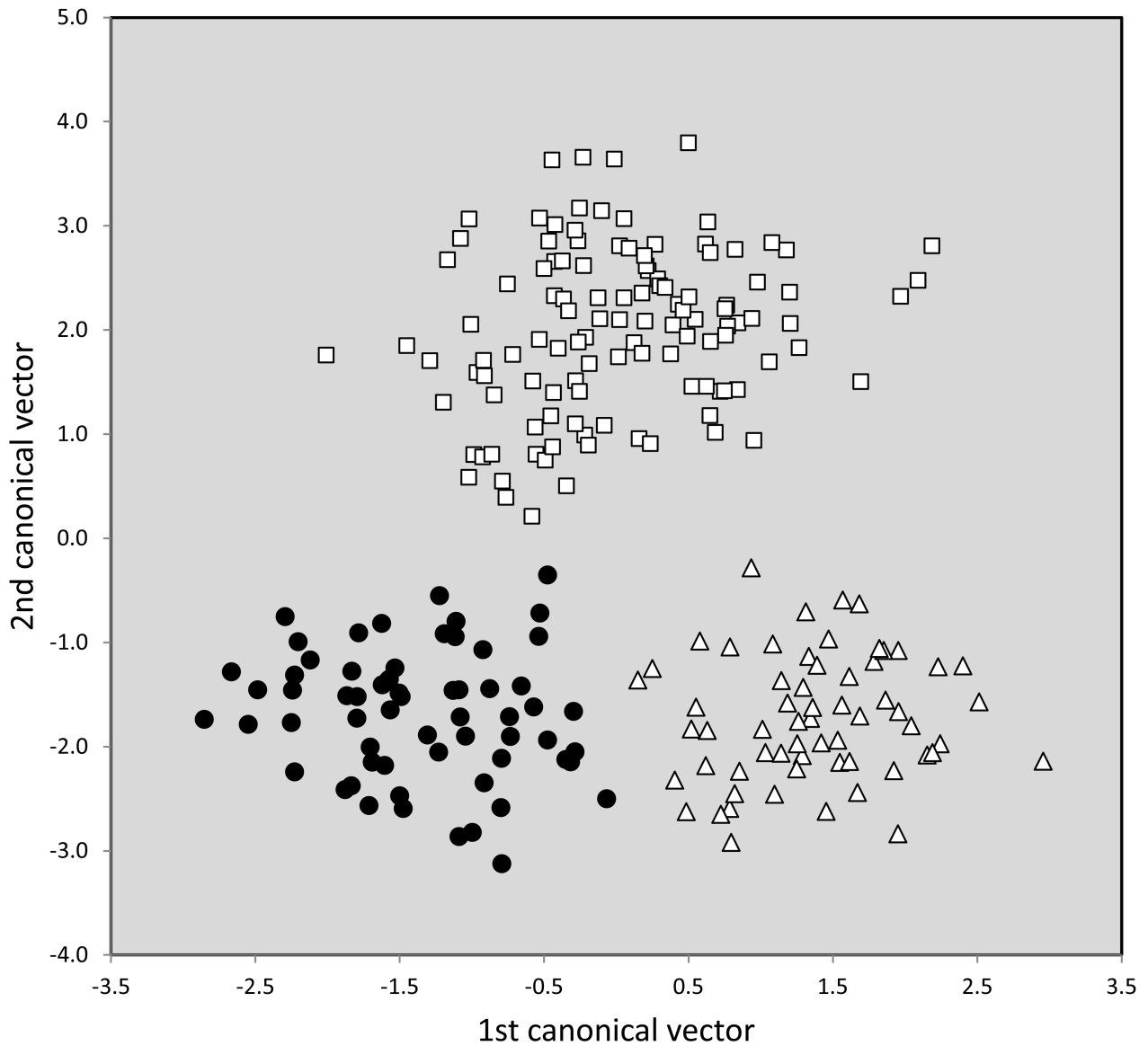
**FIGURE 44.** Separation of worker nest sample means of *Tapinoma ibericum* (black dots), *T. darioi* (white triangles) and *T. magnum* (white squares) by a linear discriminant function considering 12 RAV-corrected phenotypical characters.
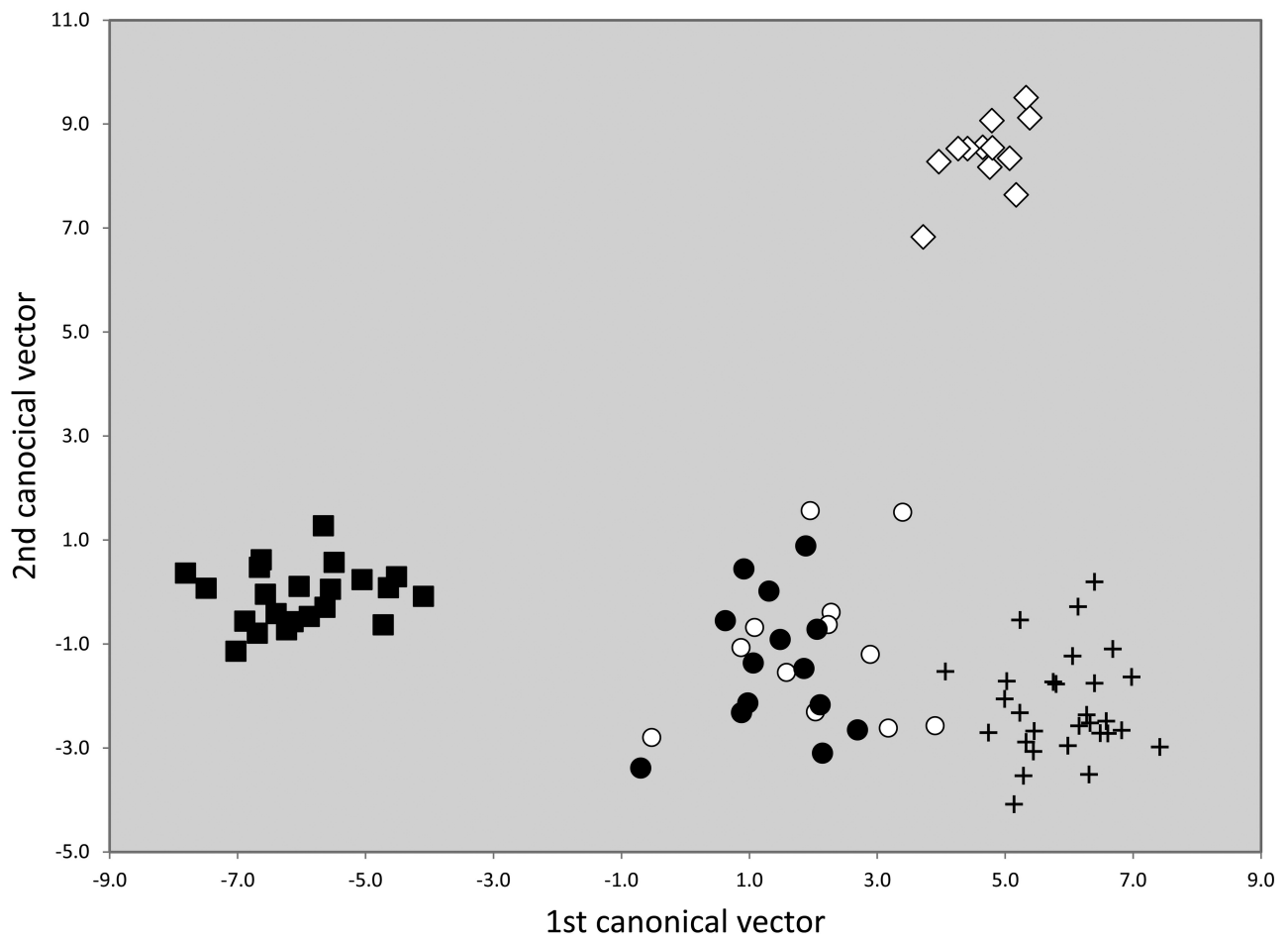
**FIGURE 45.** Comparison of the NUMOBAT-based classification of five species of the *Tapinoma nigerrimum* group with the genetic classification based on 15 microsatellite loci. Method: the first four principal components extracted from microsatellite data of 805 samples were used as characters in a linear discriminant function with the NUMOBAT-based classification imposed as species hypothesis. *T. nigerrimum* (white rhombs), *T. magnum* (black squares), *T. darioi* (crosses), *T. hispanicum* **n. sp.** (white dots) and *T. ibericum* (black dots).
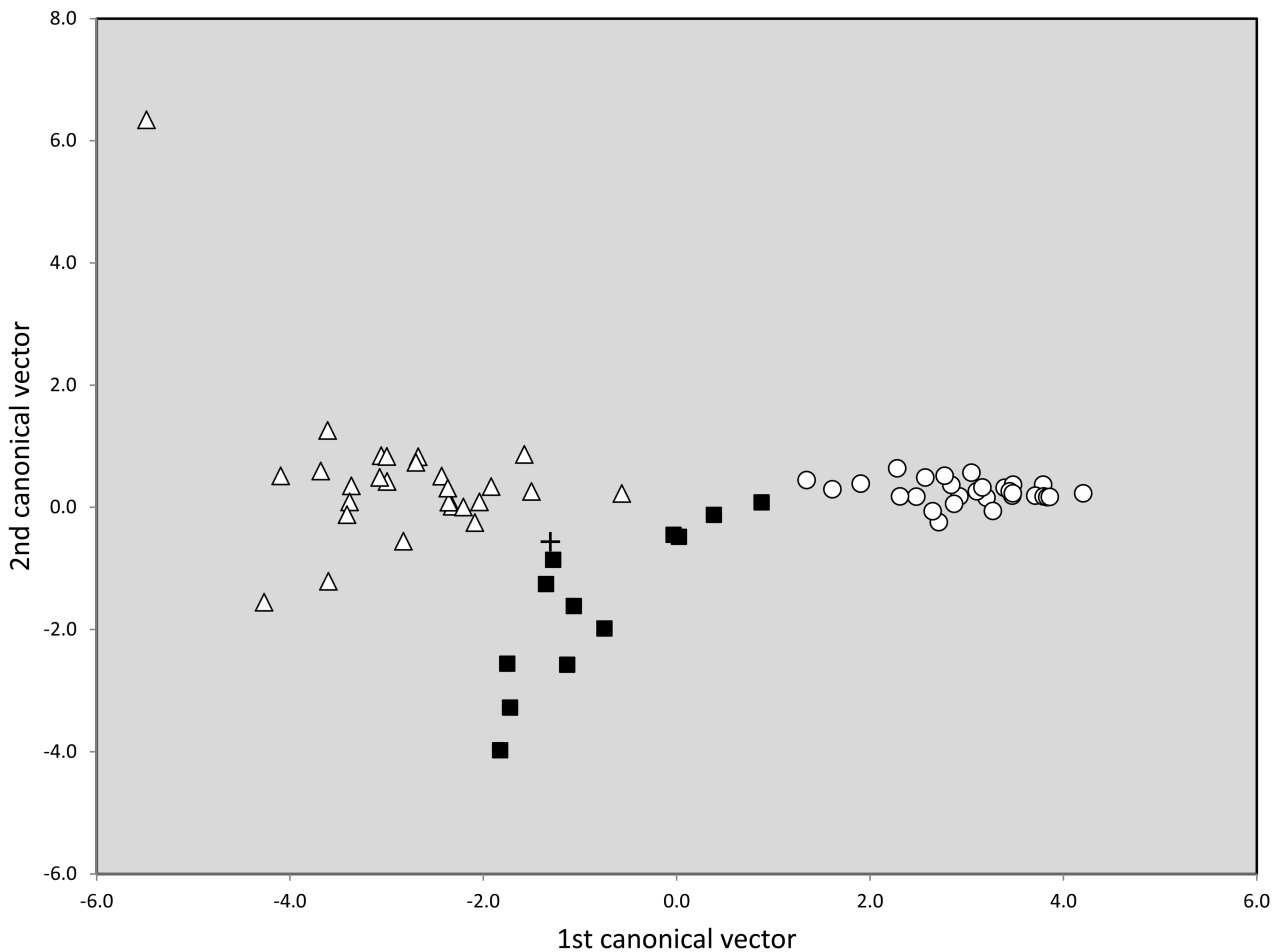
**FIGURE 46.** Comparison of the NUMOBAT-based classification of *Tapinoma ibericum* (white triangles), *T. hispanicum* **n. sp.** (black squares), *T. darioi* (white dots) and of a problematic sample (cross, see main text) with the genetic classification based on 15 microsatellite loci. Method: the first three principal components extracted from microsatellite data of only the shown 69 samples were used as characters in a linear discriminant function with the NUMOBAT-based classification imposed as species hypothesis.

### *Tapinoma hispanicum* **n.sp.**

Etymology: meaning "Spanish", because the species is known so far from only Spain.

**Type material:** Holotype plus three paratype worker on the same pin labelled "SPA:37.37503°N, 2.85169°W, Prado del Rey, 2010 m, Sierra de Baza, Ruano & Tinaut 2021.10.20 -1" and "Holotype (top) and paratypes of *Tapinoma hispanicum* Seifert" ; 12 paratype workers on three pins with same locality and date but with sample numbers 3, 4 and 7; depository SMN Görlitz.

A wild-card run in a 5-class LDA considering the five morphologically separable entities of the *T. nigerrimum* species complex allocates the holotype sample with p=0.982 to the *T. hispanicum* cluster.

**Material examined**. Numeric phenotypical data were taken in 27 nest samples with 88 workers. They all originated from Spain. For details see supplementary information SI1, SI2.

**Geographic range**. So far known from twelve sites in southern Spain delimited by 36.90°N, 38.35°N, 4.04°W, 1.49°W and with altitudes ranging from 391 to 2600 m.

**Diagnosis**:—Worker (Tab. 3, Figs. 27–29): All shape ratios given below are, in contrast to those in Tab. 3, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Large, CS 920 ± 143 μm. Head broad CL/CW 1.033 ± 0.054. Postocular distance rather small and excavation of hind margin of vertex large, PoOc/CL 0.386 ± 0.011, ExOcc 2.28 ± 0.85%. Anteromedian clypeal excision very deep and wide, ExCly/CS 10.47 ± 0.94%, ExClyW 6.91 ± 0.67%. The posterior, semicircular end of clypeal excision forms a

concave plane delimited by a sharp ventral and a less sharp dorsal edge. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge very large, nExCly 18.0 ± 6.3. Scape shorter than in related species, SL/CS 0.925 ± 0.040. Minimum distance of the inner margins of antennal socket rings moderately large, dAN/CS 0.300 ± 0.007. Eye smaller than in the supercolonial related species, EL/CS 0.229 ± 0.013. Metanotal groove shallower than in $T.$ $nigerrimum$, MGr/CS 2.81 ± 0.76 %. Mesosoma shorter and narrower than in the supercolonial related species, ML/CS 1.219 ± 0.032, MW/CS 0.613 ± 0.014. Second funiculus segment shorter than in the supercolonial related species, Fu2L/CS 13.67 ± 0.45 %, IFu2 1.828 ± 0.081. All body parts including appendages covered by a rather dense pubescence. Setae on dorsal and lateral surfaces of head and mesosoma absent. Long setae are found on hind margin of 3rd and 4th gaster segment, ventral parts of coxae and anterior clypeus. All body parts blackish brown. Mandibles, edge of clypeus and sometimes antennal funiculus and tarsi with an orange or reddish color component.

**Taxonomic comments.** The clear NUMOBAT separation of workers from the morphologically and ecologically similar *Tapinoma nigerrimum* has been shown above. *T. hispanicum* **n. sp.** differs from that species in particular by lower SL/CS$_{900}$, larger ExCly/CS$_{900}$, and lower MGr/CS$_{900}$. The genetic data provided in Fig. 46 do also support a separate species status. Furthermore, Lenoir *et al*. (2023) investigated the cuticular hydrocarbon pattern of populations in the Sierra Nevada above 2000 m altitude and found it to differ strongly from the four other species of the *T. nigerrimum* group.

**Biology.** No supercolonies have been observed so far in this species. Colonies are apparently monodomous. With exception of a roadside in an olive plantation and an urban park, all nests were found in natural or semi-natural open habitats showing a high percentage of bare ground. These habitats were usually covered by lacunar dwarf shrubs or dilute xerothermous grassland. No European *Tapinoma* species showed such a clear preference of high-altitude habitats: only 36 % of the sites were situated within 391–1206 m but 64% within 2005–2600 m. The latter habitats were as a rule extremely rocky and wind exposed.


## *Tapinoma magnum* Mayr 1861

*Tapinoma magnum* Mayr 1861 [type investigation]
The species has been described from Pisa, Italy. Investigated was the lectotype male labelled "Savi Pisa", "T. nigerrim. Magnum det. Mayr" [both labels in Mayr's handwriting], "Lectotype *Tapinoma magnum* (Mayr, 1861) des. Seifert 2012" and "AntWeb CASENT 0915547". One paralectotype gyne on another pin labelled "Savi Pisa", "T. nigerrim. Magnum det. Mayr" [both labels in Mayr's handwriting] and "Paralectotype *Tapinoma magnum* (Mayr, 1861) des. Seifert 2012". Both specimens are stored in NHM Wien. The allocation of the two type specimens to the corresponding species cluster was shown by Seifert *et al*. (2016).

**Material examined**. Numeric phenotypical data were taken in 122 nest samples with 375 workers. They originated from Algeria (10 samples), Austria (1), Azerbaijan (1), Belgium (1), France (27), Great Britain (2), Germany (27), Greece (5), Italy (32), Morocco (7), Netherlands (4), Spain(1), Switzerland (3) and Tunisia (1). For details see supplementary information SI1, SI2.

**Geographic range**. *Tapinoma magnum* has by far the widest distribution among the three supercolonial species of the *T. nigerrimum* group. It is easily spread through transport of potted plants and trees over the Mediterranean which already should have happened during the time of the Roman Empire with materials coming over from Africa. This complicates the assessment of the natural range of origin. Yet, it seems that range expansion started from North Africa and South Italy and reached North Italy and southernmost France. The colonization of South England, North France, the Benelux countries, Germany, Switzerland, and Austria is a very recent phenomenon. It started in about 1990 as a consequence of the intensification of international trade with rapid road transport and the mood of northern citizens to place big pots of Mediterranean plants in their gardens and court yards. The near absence of *T. magnum* from Spain (only one site south of Seville known) and rarity in the French Mediterranean coast is probably explained by strong competition through *T. ibericum* and *T. darioi*. It is puzzling that no findings are known so far from Asia Minor and the East Mediterranean. According to current state of information, the colonization of a city park in Baku / Azerbaijan appears to be an outlier. The altitudinal distribution of 122 nest sites is 134 ± 211 [-15, 1509] m with 97% of the findings made below 600 m.

**Diagnosis**:—Worker (Tab. 3): All shape ratios given below are, in contrast to those in Tab. 3, primary ratios

without RAV and all data are given as arithmetic mean ± standard deviation. Large, CS 963 ± 148 μm. Head broad CL/CW 1.049 ± 0.057. Postocular distance rather small and excavation of hind margin of vertex large, PoOc/CL 0.374 ± 0.012, ExOcc 1.81 ± 0.97%. Anteromedian clypeal excision less deep than in related supercolonial species and rather wide, ExCly/CS 8.72 ± 1.03%, ExClyW 6.64 ± 0.73%. The posterior, semicircular end of clypeal excision forms a concave plane delimited by a sharp ventral and a blunt dorsal edge. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge very large, nExCly 15.1 ± 5.6. Scape longer than in related supercolonial species, SL/CS 0.968 ± 0.041. Minimum distance of the inner margins of antennal socket rings larger than in related supercolonial species, dAN/CS 0.310 ± 0.008. Eye moderately large, EL/CS 0.256 ± 0.013. Metanotal groove deeper than in related supercolonial species, MGr/CS 4.20 ± 0.90%. Mesosoma rather long and wider than in related supercolonial species, ML/CS 1.291 ± 0.030, MW/CS 0.644 ± 0.019. Second funiculus segment longer than in related supercolonial species, Fu2L/CS 14.79 ± 0.47%, IFu2 1.928 ± 0.092. All body parts including appendages covered by a rather dense pubescence. Setae on dorsal and lateral surfaces of head and mesosoma absent. Longe seta are found on hind margin of 3rd and 4th gaster segment, ventral parts of coxae and anterior clypeus. All body parts blackish brown. Mandibles and edge of clypeus sometimes with an orange or reddish color component.

**Taxonomic comments.** The very clear phenotypical and genetic separation from other species of the *T. nigerrimum* group has been shown above (Figs. 44, 45).

**Biology.** The following combined properties of *T. magnum* imply a big invasive potential in urban or ruderal areas of Central Europe: (a) sufficient frost resistance, (b) the quick development of local dominance due to supercolonial life style and fighting techniques (c) a broad food spectrum which is additionally extended by worker polymorphism, (e) intranidal mating and (f) a physiological potential for long-range dispersal flight and independent single-queen colony foundation. Considering that all populations in England, the Benelux countries, Central Europe and in France north of 45.8°N have been founded by anthropogenous introduction, *T. magnum* had a share of 75.5% within 49 introduced populations, followed by *T. ibericum* (16.3%) and *T. darioi* (8.2%). The most important beachheads for introduction are garden centers and tree nurseries followed by botanical gardens. It became an important pest in settlements by digging up large amounts of sand from under pavements and kerbs, and by affecting garden plants through promotion of trophobionts. In the Netherlands it also forages in houses, ascending to the upper floors (Van Boesschoten *et al*. 2017). Colonies survived in Germany cold winters including a 14-days frost period with mean air temperatures of -6.6°C and an absolute minimum of -15°C without any visible damage. In the Mediterranean particularly abundant in open unstable or degraded areas with significant to very strong anthropogenic influence and a weakly developed tree layer. Typical for coastal areas and frequent in city centers. It prefers more sandy soils and is less abundant on rock. If reports from S France (Bernard 1968, 1983), should largely refer to *T. magnum*, it shows a quite developed tolerance against flooding, occurs in high numbers on irrigated clay soils in areas of market gardening and is found even in swampy habitats. Rather outstanding appears the high-altitude population in the Djurdjura National Park / Algeria (36.463°N, 4.178°E, 1509 m) that was found in an open situation with *Juniperus*, *Ilex* and *Rosa* within a mixed Pine-Cedar-Oak forest. Density data are missing. In the Mediterranean it is locally an eudominant species accounting for 95% of ants in some sites. Nests are subterranean and often very extended, frequently reaching to a depth of 1 m. Nest entrances typically develop to big crater-like domes of ejected soil particles (Seifert 2018). Nesting also in basements of buildings. Colonies usually develop big supercolonies stretching over areas of up to 20 hectares with millions of workers and a permanent exchange of brood between the nests via above-ground trails and subterranean tunnels. Single nests may contain up to 350 queens. Alates were observed in Algeria, Italy, France, Germany and the Netherlands 7 May ± 27 d [2 Apr, 23 Jun] n=11—this is apparently the main period. Swarming occurred in May and June, not earlier than 2–3 weeks after eclosion from pupae. Alates were also observed in August to September. Most mated gynes stay in or near to the home colony seeking adoption in conspecific nests but their big bodies and well-developed flight muscles indicate a potential ability for long-range dispersal flight and independent colony foundation. One flight observed in the Netherland 31 May 2014 took place 9:23 h Solar Time (Noordijk 2016). The German and Dutch populations (Heller 2011, Noordijk 2016) showed the last activity in late December at 3°C air temperature (cloudy days) or -2°C (sunny days). Activity was resumed after snowmelt in January at mean and maximum air temperatures of 10.6 and 12.2°C (cloudy days) or at maximum temperatures of 6.5°C during a sunny day. *T. magnum* was observed in Italy to cause severe injuries in horseradish plants in order to imbibe phloem sap (Seifert 2018). similar observations were made on tomato and zucchini stems and leaves in France. It rears root aphids in large numbers, which allows it to thrive in open, grass-dominated parks, gardens and semi-natural habitats (repeated pers. obs. of Kaufmann). *T.*

*magnum* is known from Corsica and S France to limit the spread of the invasive *Linepithema humile*. In space and food competition assays, *T. magnum* was more efficient in both interference and exploitative competition, clearly superior in direct fight, dominated food in 100% of the replicates after 1h and invaded *Linepithema* nests while the reverse was never observed (Blight *et al*. 2010). *Tapinoma magnum* is potentially superior to any ant species of open land but the final winner is determined by both fighting and recruiting properties as well as ecological adaptation and demographic factors. The displacement from food sources by *Pheidole pallidula* has to be seen in this context. The investigations of Pavan & Trave (1958) on highly toxic anal gland secretions, attributed by them to *Tapinoma nigerrimum* and later referenced by Blum & Hermann (1978) under the same name, were obviously not done in this species because of the Italian collecting site and because the enormous mass of ants ("environ 15 kg d 'ouvrières") used for the chemical analysis could only be harvested from a supercolony. Most probably the species under study was *Tapinoma magnum* which is according to our data more abundant in the region of Pavia than *T. darioi*. Blum & Hermann (1978) suggested that the iridodials, which can polymerize rapidly, may serve as carrier or fixative for the more volatile ketones in the secretion thus increasing their toxicity. Strong intraspecific aggressivity between polydomous colonies of *T. magnum* in garden centers of Germany suggests repeated introductions to the same site but artificially isolated colony fragments developed a significant aggression between former nest mates already 6 months after separation (Seifert 2018). Protection of vine and citrus mealybug colonies by *T. magnum* significantly reduced the effect of several parasitoids and predators with the exception of adult Coccinellidae (Mansour *et al*. 2012).

## *Tapinoma ibericum* Santschi 1925

*Tapinoma nigerrima* var. *ibericum* Santschi 1925 [type investigation]
The species has been described from Pozuelo de Calatrava, Spain based on a male. Investigated was the type male labeled "Type", "Tapinoma nigerrimum Nyl. ibericum Sants. type" [Santschi's handwriting], "POZUELO La Fuente" and "ANTWEB CASENT 0911578", NHM Basel. The type was remounted and the genital prepared in an in-situ position. The allocation of the type specimen to the corresponding species cluster was shown by Seifert *et al*. (2016) in an analysis of male characters.

**Material examined**. Numeric phenotypical data were taken in 63 nest samples with 211 workers. They originated from France (1 sample), Germany (3), Great Britain (1), Netherlands (4), Portugal (6), and Spain (48). For details see supplementary information SI1, SI2.

**Geographic range**. The natural range is apparently restricted to the Iberian Peninsula. Populations north of the Pyrenees in France, Germany, the Netherlands and south England (Isle of Wight) have been founded by anthropogenous introduction with plant material from Iberia. The northernmost known site, a supermarket in Burgdorf / Germany, is situated at 52.45°N and 10.00°E. Fifty-four nest sites in Iberia were situated at elevations of 623 ± 264 [7, 1264] m.

**Diagnosis**:—Worker (Tab. 3): All shape ratios given below are, in contrast to those in Tab. 3, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Large, CS 977 ± 165 µm. Head broad CL/CW 1.032 ± 0.063. Postocular distance rather small and excavation of hind margin of vertex large, PoOc/CL 0.373 ± 0.010, ExOcc 2.25 ± 1.03%. Anteromedian clypeal excision deeper than in related supercolonial species and rather wide, ExCly/CS 10.47 ± 0.36%, ExClyW 6.53 ± 0.75%. The posterior, semicircular end of clypeal excision forms a concave plane delimited by a sharp ventral and a blunt dorsal edge. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge very large, nExCly 18.80 ± 7.2. Scape moderately long, SL/CS 0.949 ± 0.047. Minimum distance of the inner margins of antennal socket rings smaller than in related supercolonial species, dAN/CS 0.292 ± 0.006. Eye moderately long, EL/CS 0.249 ± 0.016. Metanotal groove moderately deep, MGr/CS 3.25 ± 0.85 %. Mesosoma rather long and wide, ML/CS 1.273 ± 0.035, MW/CS 0.630 ± 0.019. Second funiculus segment shorter than in the supercolonial related species, Fu2L/CS 14.15 ± 0.53%, IFu2 1.898 ± 0.100. Pubescence, seta and pigmentation conditions as in *T. magnum*.

—Male (Fig. 6): the separation from the other species of the *nigerrimum* group by simple eye inspection of the genital appears difficult. However, the species can be separated by morphometry of the genital (Seifert *et al*. 2014).

**Taxonomic comments.** The phenotypical and genotypical separation from other species of the *T. nigerrimum* group has been shown above (Figs. 42, 44–46).

**Biology.** Overall biology, effect on habitat, supercoloniality, interference potential and ecological impact in the introduction area is fully comparable to *T. magnum*. The lower total frequency of introduction to the north is probably less a question of specific biology but more a result of the geographic spacing of the trade lines leading to invasion of preferentially only NW Europe. In northern areas of introduction, it is not only an outdoor species but also occurring as nuisance in buildings. The nest construction is largely subterranean and often very extended. Nest entrances typically develop to big crater-like domes of ejected soil particles. Mounds of soil particles may be constructed at spots with a higher herb layer. Alates were observed in the nests 15 May ± 28 d [24 April, 15 June] n = 5. Knowledge on foraging is sparse. Portuguese populations began to forage in February at air temperatures of 10 °C. Morris *et al*. (2002) showed that *T. ibericum* was main predator of the Olive Moth *Prays oleae* (Bern.) in southern Spain but praying on egg-parasitoids of this moth may cause an opposite economic effect (Pereira *et al*. 2004). Alvarez *et al*. (2023) suggested that it may potentially contribute to control olive pests without posing a risk to other natural enemies because it is usually not a hyper-predator. Yet, the role of *T. ibericum* differs between the crop species and depending on local conditions. Major damage by a huge supercolony (SaNo 579) is documented in a 200-ha walnut plantation in Herdade da Toula / Portugal. According to B. Leblanc (pers. comm. 2021) the damage was performed by (1) eating buds of young trees, (2) injuring young sprouts of older trees and imbibing their sap, (3) reducing pollination of fruits by eating pollen and by walking on flowers (which prevents the pollen to penetrate the pistil correctly), (4) fostering aphids, (5) killing predators of aphids and (6) extinguishing other ants.

## *Tapinoma darioi* Seifert *et al.* 2016

*Tapinoma darioi* Seifert *et al*. 2016 [type investigation]
The species has been described from Rome, Italy. Investigated was the holotype, a major worker on the same pin with three paratype workers, labelled "ITA: 41.69858° N, 12.34985° E, Roma, Castelporziano, 1 m, Grotta di Piastra, dune, D'Eustacchio 20140423 - TLa45", "Holotype (top specimen) and paratypes *Tapinoma darioi* Seifert & al."; two paratype gynes and two paratype males on other pins with the same collecting data; all material stored in SMN Görlitz. The allocation of the type specimens to the corresponding species cluster was shown by Seifert *et al*. (2016). In the extended present material, a wild-card run in a 5-class LDA considering the five morphologically separable entities of the *T. nigerrimum* species complex allocated the holotype sample with p=0.9873 to the *T. darioi* cluster.

**Material examined**. Numeric phenotypical data were taken in 61 nest samples with 210 workers. They originated from France (24 samples), Italy (13), Netherlands (1) and Spain (23). For details see supplementary information SI1, SI2.

**Geographic range**. According to the present state of information, *Tapinoma darioi* is continuously distributed along coastal areas (or near-coastal areas) of the Mediterranean Sea from Castellon (40.0°N, 0.0°E) northeast over Catalonia, the whole French coast east to Toulon, the Tyrrhenian coast of Italy from about 44.5°N south to 41°N, the Balearic Islands and Corsica. Three findings in Spain south of 37.5°N are far outside the main distribution range and certainly introductions. The only known introduction sites with established populations north of the Mediterranean zone are Limonest (45.82°N, 4.77°E), Chalon Sur Saone (46.78°N, 4.86°E), Illzach (47.77°N, 7.39°E) and Wageningen (51.98°N, 5.67°E). It is the *T. nigerrimum* group species occurring in the lowest altitudes: 61 findings range 80 ± 169 [0, 722] m, with 92% of all findings below 400 m. As a rule, occurrence more than 15 km away from the coast is rather rare in France (Centanni *et al*. 2022) but is more often observed in Catalonia.

**Diagnosis**:—Worker (Tab. 3): All shape ratios given below are, in contrast to those in Tab. 3, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Smallest species of the *T. nigerrimum* group, CS 897 ± 135 µm. Head broad CL/CW 1.052 ± 0.052. Postocular distance rather small and excavation of hind margin of vertex large, PoOc/CL 0.380 ± 0.010, ExOcc 2.07 ± 0.85%. Anteromedian clypeal excision large and rather wide, ExCly/CS 9.71 ± 0.93%, ExClyW 6.14 ± 0.74%. The posterior, semicircular end of clypeal excision forms a concave plane delimited by a sharp ventral and a blunt dorsal edge. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge large, nExCly 14.43 ± 5.7. Scape moderately long, SL/CS 0.965 ± 0.037. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN/CS 0.300 ± 0.007. Eye moderately large, EL/CS 0.253 ± 0.014. Metanotal groove moderately deep, MGr/CS 2.80 ± 0.83 %. Mesosoma rather long and wide, ML/CS 1.274 ± 0.031, MW/CS 0.632 ± 0.021. Second

funiculus segment longer than in the supercolonial related species, Fu2L/CS 14.50 ± 0.44%, IFu2 1.961 ± 0.106. Pubescence, seta and pigmentation conditions as in *T. magnum*.

**Taxonomic comments.** The phenotypical and genotypical separation from other species of the *T. nigerrimum* group has been shown above (Figs. 42, 44–46).

**Biology.** Typical habitats are open unstable or degraded areas with very strong anthropogenic influence and a weakly developed tree layer but, in difference to *T. magnum* more frequently occurring in natural or semi-natural sand dunes. Niche separation is evident in Castelporziano Presidential Estate / Italy where *T. darioi* solely occurs on dunal systems while *T. magnum* is mainly linked to the Mediterranean scrub in much structured environments (D'Eustaccio *et al*. 2019). The nest construction is subterranean and often very extended, frequently reaching to a depth of 1 m. Nest entrances typically develop to big crater-like domes of ejected soil particles. Density data are missing. In the Mediterranean it is locally a eudominant species accounting for 95% of ants in some sites. Extremely polygynous and polydomous resulting in large supercolonies. The lower frequency of anthropogenous introduction in the Benelux countries and Germany is probably no question of specific biology but a result of the geographic spacing of the shipping of goods. It was observed in S France to limit the spread of the invasive *Linepithema humile* (Blight *et al.* 2010).

Alates were observed in the nests 22 May ± 20 d [23 Apr, 23 Jun] n = 12. The age and role of sexuals occasionally observed in September is unknown. Mating is probably intranidal or within the area of the supercolony. Foraging and nutrition was studied by (Xerda *et al*. 1989) in lowland Spain. Foraging is diurnal from February to May and crepuscular and nocturnal from June to November. Very extensive trophobiosis with aphids occurs both on high trees, in the herb layer and the rhizophere; a permanent, 24-hour presence at aphid colonies was observed in less sun-exposed habitat spots. Honeydew accounts for probably >80% of total food mass. Nectarivory, though frequently observed with different plants, provides a very low contribution to energetic input. Plant parts are not consumed with the exception of elaiosomes of diverse myrmecochorous plants (e.g., *Centaurea aspera*, *Euphorbia characias*) and of fallen sweet fruits. Carnivory of insects, snails and spiders is significant (perhaps 15% of total food mass) and probably more a collecting of carcasses than active hunting. Predation of sexuals of ants alighting after nuptial flight may be intensive. The mean and maximum size of solid food items retrieved by single workers are 2.6 and 6 mm. After discovery of very large food items mass recruitment starts, the item is disintegrated and the cut-off pieces are retrieved by single workers. Cooperative transport of items is so far unknown. Tool use: occasionally small twigs or pebbles are dropped into liquid food and retrieved after impregnation. In northern areas of introduction, it is not only an outdoor species but also occurring as nuisance in buildings.

### *Tapinoma simrothi* Krausse-Heldrungen 1911

*Tapinoma erraticum* var. *simrothi* Krausse-Heldrungen 1911 [neotype fixation]
Krausse-Heldrungen (1911) gave no type locality but concluded from the title of the paper the terra typica is Sardinia. Original types of *T. simrothi* are missing and the full text of Krausse-Heldrungen's description allows only the conclusion that it is bigger than *erraticum*: "Klopfte ich von Wolfsmilchblüten; sie gleicht dem *T. erraticum* Ltr., nähert sich in der Grösse aber dem *T. erraticum-nigerrimum*" (Krausse-Heldrungen 1911, p18). The existence of four cryptic species within the *Tapinoma simrothi* complex and necessity for clear reference specimens requires the fixation of a neotype. Even though there is, due to missing taxonomic knowledge in the past, no name tradition to be saved, we decided against placing the name under Incertae Sedis. Thus a neotype was fixed in a worker from a nest sample with males, gynes and other workers, labelled " ITA:38.92561°N, 8.71653°E, Teulada-6 Km S-W, 2 m, open area in gariga under Cynara cardunculus, Centorame 20140417-TSa17"; depository SMN Görlitz. The neotype sample is allocated with p = 1.000 to the *T. simrothi* cluster in a LDA considering all four species of the *T. simrothi* group.

*Tapinoma minor* Bernard 1945 [evaluation of type image and zoogeography]
This taxon has been described from the forest of Mamora near Ain Assou (34.17°N, 6.19° W, 93 m).
The image of a type specimen labelled "Mamora 1t 10 daya VI F.Bernard det., 42" [Bernard's handwriting], "Tapinoma minor 1942. Type" [Bernard's handwriting] and "ANTWEB CASENT 0913749" was investigated with

making attempts to correct for measurement reductions produced by inadequate viewing positions. The following data could be derived: CS 655 µm, CL/CW 1.223, PoOc/CL 0.417, ExOcc/CS 0 %, SL/CS 1.003, ExCly/CS 10.52 %, ExClyW/CS 5.77 %, ExClL/W 1.823, dAN/CS 0.292, MGr/CS 3.47 %, MW/CS 0.659, Fu2L/CS 14.68 %, IFu2 1.489. When plotting all these shape variables against CS, each character is fully within that part of the cloud of *T. simrothi* & *T. insularis* **n. sp.** workers formed by the smallest individuals. Yet, a decision as to which of these two species the *T. minor* type should belong is not possible due to the lower accuracy of image-derived morphometry and lower reliability of single-specimen indication. The synonymization with *T. simrothi* is stated here because the type locality of *T. minor* is within the geographic range of *T. simrothi* but 1300 km west of the western range border of *T. insularis* **n. sp.** and in a natural habitat far away from a sea harbor.

**Material examined**. Numeric phenotypical data were taken in 40 samples with 121 workers. They originated from Algeria (1 sample), France (1), Italy (11), Morocco (4), Portugal (6), Spain (16) and Tunisia (1). For details see supplementary information SI1, SI2.

**Geographic range**. West Mediterranean species, natural range reaching over 2000 km from Morocco (30°N, 10°W) east to Tunisia (35.7°N, 10°E) and going north to 41°N in Spain and Sardinia. The potential for anthropogenous spreading is apparently much lower than in the supercolonial species of the *T. nigerrimum* group. Yet, the northernmost known record from Faillant / France (43.489°N, 6.355°E) found in a small urban green within a strongly paved area should have been founded by anthropogenous introduction. The altitudinal range of 40 findings is characterized by 251 ± 379 [1, 1555] m with the highest site found in the Moroccan Atlas Mountains.

**Diagnosis**:—Worker (Tab. 5): All shape ratios given below are, in contrast to those in Tab. 5, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Medium-sized, CS 870 ± 94 µm. Head moderately elongated, CL/CW 1.094 ± 0.043. Postocular distance and excavation of hind margin of vertex rather large, PoOc/CL 0.395 ± 0.010, ExOcc 1.50 ± 0.82%. Anteromedian clypeal excision very deep and narrow, ExCly/CS 12.74 ± 0.93%, ExClyW 6.01 ± 0.82%. The edge of clypeal excision curves slightly down below the level of adjacent clypeal surface, thus appearing rather blunt. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge moderately large, nExCly 7.0 ± 3.5. Scape longer than in *T. insularis* **n. sp.**, SL/CS 0.961 ± 0.026. Minimum distance of the inner margins of antennal socket rings rather small, dAN/CS 0.288 ± 0.006. Eye moderately long, EL/CS 0.253 ± 0.011. Metanotal groove moderately deep, MGr/CS 3.05 ± 0.68%. Mesosoma rather long and moderately wide, ML/CS 1.278 ± 0.032, MW/CS 0.636 ± 0.019. Second funiculus segment rather short, Fu2L/CS 13.46 ± 0.44%, IFu2 1.687 ± 0.106. All body parts including appendages covered by a moderately dense, short pubescence. Body surfaces more shiny than in the *T. nigerrimum* group. Setae on dorsal and lateral surfaces of head and mesosoma and on first two gaster tergites absent. Long seta are found on hind margin of 3rd and 4th gaster tergite, all gaster sternites, ventral parts of coxae and anterior clypeus. All body parts blackish brown. Mandibles and edge of clypeus sometimes with an orange or reddish color component.

—Male (Fig. 7): the separation from the other species of the *simrothi* group by simple eye inspection of the genital appears difficult. Yet, a morphometric study appears promising when enough data will be available.

**Taxonomic comments.** The *Tapinoma simrothi* group contains four cryptic species separable by NUMOBAT: *T. simrothi* , *T. insularis* **n. sp.**, *T. phoenicaeum* and *T. karavaievi* . Sufficient microsatellite data were available for the first three species and these genetic data confirmed the NUMOBAT classifications. Within a total of 43 samples for which both NUMOBAT and microsatellite data were available, the agreement of phenetic and genetic classification was 100%. Below we describe the run of exploratory and hypothesis-driven data analyses.


Block 1: Species hypothesis formation based on NUMOBAT data
The morphological separation of the four entities was done in several steps. In the first step of analysis all 16 NUMOBAT characters (CS and 15 RAV-corrected characters) were run unselectively in NC-part.kmeans and NC-Ward (Fig. 47). The analysis of 132 samples revealed two big branches—one composed of clusters with West and Central Mediterranean distribution (later identified as *T. simrothi* and *T. insularis* **n. sp.**) and another one collecting clusters with more eastern distribution (later identified as *T. phoenicaeum* and *T. karavaievi*). The classification of both exploratory data analyses for K=2 disagreed in 5.3% of the 132 samples. The final hypothesis for K=2 was determined by a controlling LDA in which the disagreeing samples were run as wild-cards. The error for K=2 was according to the controlling LDA 2.3% in NC-part.kmeans and 3.8% in NC-Ward.
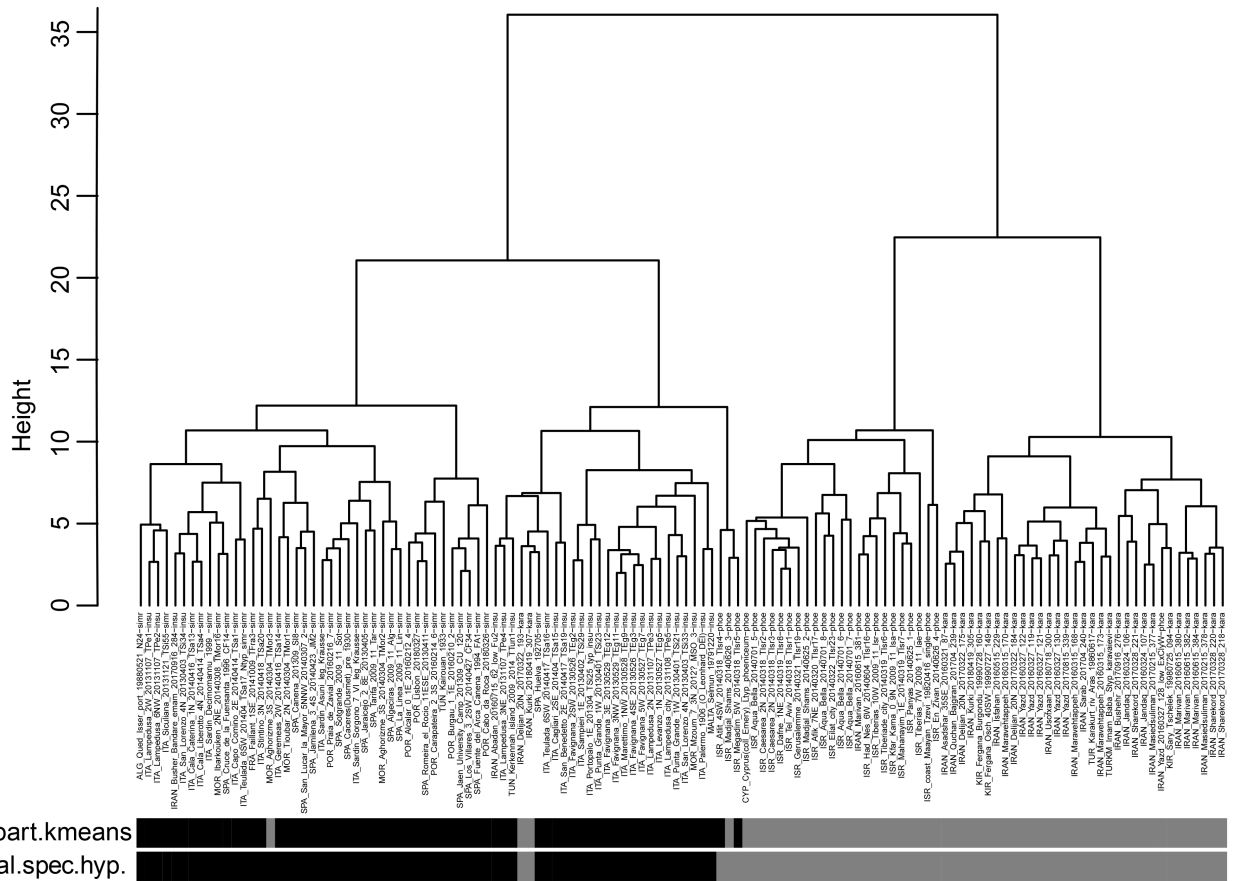
**FIGURE 47.** Demonstration of two main clusters within worker nest samples of the *Tapinoma simrothi* group by NC-Ward and NC-part.kmeans clustering considering 16 RAV-corrected phenotypical characters. Black cluster—*T. insularis n.sp.* et *T. simrothi*; gray cluster—*T. phoenicaeum* et *T. karavajevi*. The classification error of NC-part.kmeans relative to the controlling linear discriminant function is 2.3% for K=2.

As next step of analysis, the western and eastern cluster were analyzed separately according to the same schedule as reported above. The western cluster with 66 samples was separated into the species *Tapinoma insulari*s **n. sp.** and *T. simrothi* (Fig.48). The classification proposals by NC-part.kmeans and NC-Ward disagreed with the controlling LDA in 1.5% and 7.6% of the samples. When run as wild-cards in a LDA, the neotype specimen of *T. simrothi* is allocated to the *T. simrothi* cluster with p=1.000 and the holotype sample of *T. insularis* **n. sp.** with p=0.9992 to the corresponding cluster.

The nest samples of the eastern cluster were separated into the species *Tapinoma phoenicaeum* and *T. karavajevi* (Fig.49). The classification proposals by NC-part.kmeans and NC-Ward disagreed with the controlling LDA in 0% and 1.5% of the samples respectively. When run as wild-cards in a LDA, the lectotype sample of *T. phoenicaeum* is allocated to its name-bearing cluster with p=0.9992 and the lectotype sample of *T. karavajevi* with p=0.9998 to the corresponding cluster.
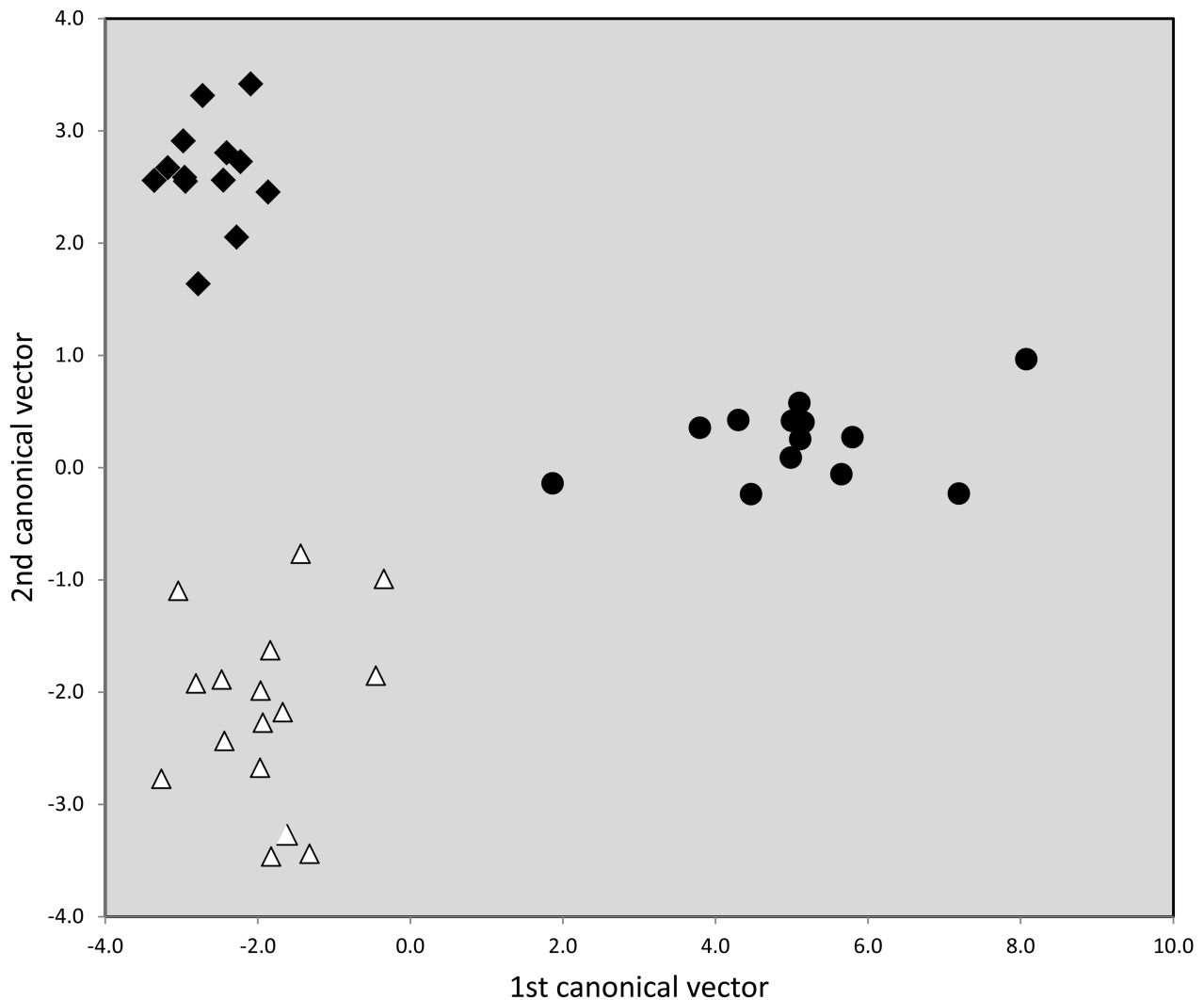
**FIGURE 48.** Separation of worker nest samples of *Tapinoma simrothi* (grey bars) and *T. insularis n.sp.* (black bars*)* by NC-Ward and NC-part.kmeans clustering considering 16 RAV-corrected NUMOBAT characters. The classification error of NC-part. kmeans relative to the controlling linear discriminant function is 1.5%.



**FIGURE 49.** Separation of worker nest samples of *Tapinoma karavajevi* (red bars) *and T. phoenicaeum* (black bars) by NC-Ward and NC-part.kmeans clustering considering 16 RAV-corrected NUMOBAT characters. The classification error of NC-part. kmeans relative to the controlling linear discriminant function is 0%.

**FIGURE 50.** Comparison of the NUMOBAT-based classification of *Tapinoma insularis* **n. sp.** (black rhombs), *T. simrothi* (white triangles) and *T. phoenicaeum* (black dots) with the genetic classification based on 15 microsatellite loci. Method: the first four principal components extracted from microsatellite data of only the shown 43 samples were used as characters in a linear discriminant function with the NUMOBAT-based classification imposed as species hypothesis.

Block 2: Confirmation of morphological species hypotheses by nuDNA data

In *Tapinoma simrothi* , *T. insularis* **n. sp.** and *T. phoenicaeum*, where sufficient microsatellite data were available, 100% of NUMOBAT classifications could be confirmed by nuclear DNA. This was established by running a LDA using the first four principal components extracted from microsatellite data as characters and imposing the NUMOBAT classifications as hypotheses (Fig.50). An overfitting of the LDA was not given as the smallest class contained 13 samples.

**Biology.** Apart from semi shaded conditions with trees such as olive plantations or cork-oak stands, *T. simrothi* prefers very sunny open habitats. These may be natural or semi natural (sand dunes, coastal cliffs, open patches in garrigue), rural (meadows, pastures, gardens, roadsides) or urban (areas with much pavement, asphalt or concrete and some greenery). *Tapinoma simrothi* is polygynous and may form both monodomous and polydomous colonies but apparently not such big supercolonies as known from species of the *T. nigerrimum* group. Nests are largely subterranean. Accurate and rather solid mounds of soil particles measuring up to 20 cm in diameter and height are typical above-ground structures in natural, semi natural and rural habitats but nests may be also under stones or in and under walls. Six observations of alates were made between 16 April and 30 May.

### *Tapinoma insularis* n. sp.

Etymology: belonging to islands, because the species is, compared to its sister species *T. simrothi*, more frequently found on islands of the Mediterranean Sea.

**Type material:** Holotype plus three paratype worker on the same pin from Sicily, labelled "ITA: 36.68176°N, 15.13684°E, Portopalo-1 km E, 46 m, D'Eustacchio 20130404-TSi25"; the sample also contained a male and a gyne; depository SMN Görlitz. If run as wild-card in a LDA considering all NUMOBAT characters, the sample is allocated with p = 0.9992 to its name bearing cluster (see above).

**Material examined**. Numeric phenotypical data were taken in 26 nest samples with 84 workers. They originated from Iran (2 samples), Italy (21), Malta (1), Morocco (1) and Tunisia (1). For details see supplementary information SI1, SI2.

**Geographic range**. The species is mainly distributed, with 90% of all findings, over the islands of the Central Mediterranean Sea between 9°E and 15.5°E: Sardinia, Sicily and Isole Egadi, Lampedusa, Kerkennah, and Malta. Two geographic outliers from Abadan (30.347°N, 48.295°E) and Busher (29.839°N, 50.255°E) refer to harbor areas at the Iranian coast of the Persian Gulf and may be interpreted as anthropogenous introductions—if not representing an unrecognized cryptic species. The altitudinal distribution of 25 samples is characterized by $27 \pm 31$ [1, 106] m.

**Diagnosis**:—Worker (Tab. 5, Figs. 38–40): All shape ratios given below are, in contrast to those in Tab. 5, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Slightly smaller than *T. simrothi*, CS $824 \pm 78$ μm. Head slightly more elongated than in *T. simrothi*, CL/CW $1.120 \pm 0.046$. Postocular distance rather large, PoOc/CL $0.401 \pm 0.009$; excavation of hind margin of vertex smaller than in *T. simrothi*, ExOcc $1.10 \pm 0.51$%. Anteromedian clypeal excision deep and narrow, ExCly/CS $11.21 \pm 0.84$%, ExClyW $5.44 \pm 0.72$%. The edge of clypeal excision curves slightly down below the level of adjacent clypeal surface, thus appearing rather blunt. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge slightly larger than in *T. simrothi*, nExCly $8.8 \pm 3.7$. Scape slightly shorter than in *T. simrothi*, SL/CS $0.954 \pm 0.029$. Minimum distance of the inner margins of antennal socket rings rather small, dAN/CS $0.293 \pm 0.006$. Eye moderately large, EL/CS $0.257 \pm 0.010$. Metanotal groove moderately deep, MGr/CS $3.24 \pm 0.71$%. Mesosoma longer than in *T. simrothi* and moderately wide, ML/CS $1.302 \pm 0.032$, MW/CS $0.640 \pm 0.019$. Second funiculus segment rather short, Fu2L/CS $13.42 \pm 0.44$%, IFu2 $1.622 \pm 0.106$. Pubescence, seta and pigmentation characters as in *T. simrothi*.

**Taxonomic comments.** The clear separation from other species of the *Tapinoma simrothi* group by NUMOBAT and nuDNA data was shown above.

**Biology.** Little information is available. Reported habitats are grassland, coastal sand dunes, house gardens, roadsides, sealed urban areas with little greenery. Alates were observed on 2 April.

### *Tapinoma phoenicaeum* Emery 1925

*Tapinoma simrothi* var. *phoenicaea* Emery 1925 [type investigation]
The species has been described from Cyprus and Greece. Investigated were 4 workers from the lectotype sample labelled "Cipro", "T.simrothi var. phoenicea Emery" [Emery's handwriting], "ANTWEB CASENT0904017", "SYNTYPUS Tapinoma simrothi phoenicea Emery, 1925". As lectotype is fixed by present designation the major worker in the sample having CW 974 μm, SL 978 μm and dAN 295 μm. Depository MCSN Genova. The lectotype sample is allocated with p=0.9992 to its name-bearing cluster if run as wild-card in LDA considering all for species of the *T. simrothi* group.

*Tapinoma simrothi pheonicium* (sic!) sensu Hefetz & Lloyd 1983)
Hefetz & Lloyd (1983) distinguished four dolichoderine ant species to occur in Israel and apparently correctly identified (but misspelled) *T. phoenicaeum* which they reported to be the most abundant dolichoderine species in Israel. This is in agreement with the current survey in which 85% of the 40 *Tapinoma* samples from Israel were classified as *T. phoenicaeum* and in addition it was the only species of the *T. simrothi* group found there.

*Tapinoma simrothi* sensu Simon & Hefetz (1991)

Despite having no voucher specimens it is highly probable for the reasons reported above that the trail pheromone investigations of Simon & Hefetz (1991) were done in *T. phoenicaeum*.

*Tapinoma israelis* sensu Berville *et al*. (2013)

Three worker samples from Israel (SaNo 137, 139 and 142) misidentified by Berville *et al*. (2013) as *T. israelis* and used in their cuticular hydrocarbon study were allocated with p>0.995 to the *T. phoenicaeum* cluster considering all 16 NUMOBAT characters and all for species of the *T. simrothi* group.

**Material examined**. Numeric phenotypical data were taken in 28 nest samples with 87 workers. They originated from Cyprus (1 sample), Iran (2) and Israel (25). For details see supplementary information SI1, SI2.

**Geographic range**. So far only known from Cyprus, 23 sites in in Israel and 2 sites in the Iran ranging east to 54.4°E. The southern range border is unknown. Images of worker ants from Wadi Hanifa / Saudi Arabia (24.67°N, 46.60°E) provided in www.antweb.org under the specimen identifiers CASENT0906355 and CASENT0919801) might belong to *T. phoenicaeum* but the low accuracy of image evaluation does not allow a safe separation from *T. karavaievi*. The wide altitudinal range of 28 samples is given by $364 \pm 465$ [-305, 1303] m.

**Diagnosis**:—Worker (Tab. 5): All shape ratios given below are, in contrast to those in Tab. 5, primary ratios without RAV and all data are given as arithmetic mean $\pm$ standard deviation. Slightly smaller than *T. simrothi*, CS $860 \pm 84$ µm. Head moderately elongated, CL/CW $1.097 \pm 0.043$. Postocular distance much smaller than in *T. simrothi*, PoOc/CL $0.377 \pm 0.013$; excavation of hind margin of vertex smaller than in *T. simrothi*, ExOcc 1.24 $\pm$ 0.75%. Anteromedian clypeal excision shallower and narrower than in *T. simrothi*, ExCly/CS 10.58 $\pm$ 0.98%, ExClyW $5.16 \pm 0.62$%. The edge of clypeal excision curves slightly down below the level of adjacent clypeal surface, thus appearing rather blunt. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge moderate, nExCly $5.6 \pm 2.4$. Scape moderately long, SL/CS $0.971 \pm 0.027$. Minimum distance of the inner margins of antennal socket rings rather small, dAN/CS $0.293 \pm 0.008$. Eye slightly smaller than in related species, EL/CS $0.248 \pm 0.010$. Metanotal groove moderately deep, MGr/CS 3.24 $\pm$ 0.73%. Mesosoma longer than in *T. simrothi* and moderately wide, ML/CS $1.301 \pm 0.029$, MW/CS $0.636 \pm 0.023$. Second funiculus segment longer than in *T. simrothi*, Fu2L/CS 13.96 $\pm$ 0.50%, IFu2 $1.668 \pm 0.089$. Pubescence, seta and pigmentation characters as in *T. simrothi*.

**Taxonomic comments.** The separation from the other three species of the *T. simrothi* group has been shown above. Berville *et al*. (2013) demonstrated differences in cuticular hydrocarbon patterns between Israelian *T. phoeniceum* (misidentified by them as *T. israelis*) and Iberian *T. simrothi*. This in line with observations of D. d'Eustacchio and M. Centorame (pers. comm. 2015) who noted, when collecting samples in the field, that the Israelian *T. phoenicaeum* caused an allergic skin reaction which they did not observe in *T. simrothi* from Morocco.

**Biology.** *Tapinoma phoenicaeum* was collected in our study in basically any natural, rural or urban habitat. Alates were observed from 4 March to 6 April. Hefetz & Lloyd (1983) described the situation in Israel as follows "It is found in the temperate zones as well as in the oases of the desert, and it is a major house pest. These ants are notorious for the large mounds, sometimes as high as half a meter, which they build during the winter. Each mound is carved with galleries forming a well-aerated solarium where the workers rear the brood. If a mound is accidentally destroyed, the ants enter in alarm frenzy, some rushing to the exposed areas with open mandibles, biting fiercely at any moving object; meanwhile other workers carry the brood to the safety of deeper undisturbed galleries. At this time a characteristic sweet smell usually permeates the air around the mound. The smell has been traced to the chemicals emanating from a pair of anal glands located at the tip of the abdomen."

## *Tapinoma karavaievi* Emery 1925

*Tapinoma simrothi karavaievi* Emery 1925 [type investigation]

This species has been described from Turkmenistan. Investigated were 4 syntype workers on the same pin labelled "Imam Baba Karavaiev", "SYNTYPUS T.simrothi karavaievi Emery, 1925" and 6 syntype workers on two other pins with similar labelling which are deposited in MCSN Genova. As lectotype is fixed by present designation a major worker with CW 970 µm and SL 929 µm placed on the top card of the first pin. The lectotype sample is allocated with p = 0.9998 to its name-bearing cluster in a LDA considering all for species of the *T. simrothi* group.

*Tapinoma simrothi ssp. azerbaidzhanica* Karavajev 1932 [image of type and zoogeography]

This taxon has been described from near the railroad station Ganja in Azerbaijan (40.713°N, 46.372°E, 345 m) on the basis of males and workers. The synonymization with *T. karavaievi* is based on evaluation of the images of the specimen CASENT0917138 in ww.antweb.org, labelled "Gandzha Azerbeidzh. Rekat.", "5416. Coll. Karavaievi", "Tapinoma simrothi ssp. azerbeidzhanica Kar. typ." [all three labels written by Karavaiev]. From Karavaievs drawings of male genitalia and the features shown by the image of the worker it is clear that the taxon belongs to the *T. simrothi* group. The imaged specimen is allocated in a wild-card run of an LDA with p=0.764 to *T. karavaievi*, with p=0.177 to *T. phoenicaeum* and with p=0.059 to *T. insularis* **n. sp.** when considering 10 absolute measurements which could be derived from the image (CL, CW, PoOc, ExOcc, dAN, ExCly, ExClyW, Fu2L, Fu2W, SL). This morphometric classification is fully in line with occurrence probabilities expected from zoogeography.

**Material examined**. Numeric phenotypical data were taken in 39 samples with 121 workers. They originated from Iran (31 samples), Kazakhstan (2), Kyrgistan (4), Turkey (1) and Turkmenistan (1). For details see supplementary information SI1, SI2.

**Geographic range**. Distributed from E Turkey (40.16°N, 42.61°E) over Azerbaijan, Iran, Turkmenistan, Kazakhstan, east to Kyrgistan (40.36°N, 72.92°E). The most southern and northern sites known are at 29.84°N, 50.26°E in Iran and 45.45°N, 64.24°E in Kazakhstan. The altitudinal range of 39 samples is given by 1107 ± 591 [29, 2075] m.

**Diagnosis**:—Worker (Tab. 5): All shape ratios given below are, in contrast to those in Tab. 5, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Slightly larger than *T. phoenicaeum*, CS 884 ± 96 μm. Head moderately elongated, CL/CW 1.077 ± 0.045. Postocular distance larger than in *T. phoenicaeum*, PoOc/CL 0.386 ± 0.010; excavation of hind margin of vertex smaller than in *T. phoenicaeum*, ExOcc 0.94 ± 0.61%. Anteromedian clypeal excision deeper and wider than in *T. phoenicaeum*, ExCly/CS 10.89 ± 0.66%, ExClyW 6.01 ± 0.70%. The edge of clypeal excision curves slightly down below the level of adjacent clypeal surface, thus appearing rather blunt. Sum of pubescence hairs and smaller setae protruding across the margin of clypeal excision including its dorsal edge moderate, nExCly 6.6 ± 2.6. Scape moderately long, SL/CS 0.973 ± 0.029. Minimum distance of the inner margins of antennal socket rings rather small, dAN/CS 0.296 ± 0.006. Eye moderately large, EL/CS 0.252 ± 0.011. Metanotal groove moderately deep, MGr/CS 3.58 ± 0.67%. Mesosoma longer than in *T. simrothi* and moderately wide, ML/CS 1.300 ± 0.038, MW/CS 0.635 ± 0.022. Second funiculus segment shorter than in *T. phoenicaeum*, Fu2L/CS 13.58 ± 0.43%, IFu2 1.676 ± 0.058. Pubescence, seta and pigmentation characters as in *T. simrothi.*

**Taxonomic comments.** The separation from the other three species of the *T. simrothi* group has been shown above.

**Biology.** The species was found in open or partially shaded natural, rural and urban habitats with sparse soil vegetation, in semidesert, farmland with irrigation, settlements and on open river banks.

The nest entrance may be surrounded by craters of ejected soil.


# *Tapinoma festae* Emery 1925

*Tapinoma simrothi festae* Emery 1925 [type investigation]

This species has been described from Rhodes / Greece based on a male and gyne. Investigated were 1 male and 1 gyne syntype labelled "Rodi", "T.simrothi festae Emery" [Emery's handwriting], "ANTWEB CASENT 0904018", "SYNTYPUS Tapinoma simrothi festae Emery, 1925"; depository MCSN Genova.

The type gyne is an unmistakable combination of rather large size (CS 1110 μm), short head (CL/CW 0.908), very shallow clypeal excision (ExCly/CS 3.75%), rather many hairs at clypeal excision (nExCly 10), broad frons (dAN/CS 0.315) and very wide mesosoma (MW/CS 1.222). The unique character combination of small CL/CW, large dAN/CS and very small EXCly/CS is repeated in workers which allows, in the absence of type workers, clearly allocating worker samples to this species (Tab. 2).

**Material examined**. Numeric phenotypical data were taken in 12 samples with 30 workers and one gyne. They originated from Greece (7 samples) and Turkey (5). For details see supplementary information SI1, SI2.

**Geographic range**. Known so far only from a small geographic region between 35 and 39.5°N, 25 and 28°E. The range includes the Greek islands Crete, Rhodos, Chios and Samos and the western coastal margin of continental Asia Minor. All sites were situated at elevations below 200 m.

**Diagnosis**:—Worker (Tab. 2, Figs. 24–26): All shape ratios given below are, in contrast to those in Tab. 2, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Slightly larger than *glabrella*, CS 808 ± 95 µm. Head much shorter than in species of similar size, CL/CW 1.030 ± 0.043. Postocular distance smaller than in species of similar size, PoOc/CL 0.383 ± 0.014. Anteromedian clypeal excision extremely shallow and very wide, ExCly/CS 3.78 ± 0.50 %, ExClyW 9.25 ± 2.08 %. Sum of pubescence hairs and smaller setae protruding a few microns across margin of clypeal excision low, nExCly 2.68 ± 1.16. Posterior margin of head in full face view in much more excavated than in other species of similar body size, ExOcc/CS 1.51 ± 0.89 %. Scape moderately long, SL/CS 0.989 ± 0.017. Minimum distance of the inner margins of antennal socket rings much wider than in other species of similar body size, dAN 0.322 ± 0.007. Eye medium-sized, EL/CS 0.267 ± 0.007. Metanotal groove moderately deep, MGr/CS 3.88 ± 0.84 %. Mesosoma moderately wide and long, MW/CS 0.678 ± 0.025, ML/CS 1.319 ± 0.026. Second funiculus segment very short, Fu2L/CS 12.47 ± 0.21 %, IFu2 1.455 ± 0.099. Seta condition, pubescence and pigmentation similar to *T. erraticum*.

**Taxonomic comments.** A view on Figs. 24–26 and Tab. 2 shows that this is one of the few *Tapinoma* species which cannot be confused.

**Biology.** In Crete, this species was observed in dry habitats such as sandy beach, stone walls in antic ruins, gardens. Nests have been seen in sun-exposed places, often simply in ground or under stones. Nest density seems to be weak. Workers were observed alone collecting dead arthropods, or forming tracks to collect mealybugs honeydew, even in the blazing sun. They show a strong tendency to flee when the nest is disturbed.

### *Tapinoma madeirense* Forel 1895

*Tapinoma erraticum* var. *madeirense* Forel 1895 [type investigation]
Forel undoubtedly has seen numerous differently labelled samples with workers and gynes from different localities in Madeira mainly collected by Schmitz. This material was later distributed to several museums (MHN Genève, NHM Basel, MCZ Cambridge, HMNH Budapest). The original description of Forel only refers to workers and mentions Ribeira Brava / Madeira as only type locality. Wetterer *et al.* (2007) designated the topmost gyne of a sample from Ribeira Brava, stored in MHN Genève, as lectotype. This lectotype fixation in a gyne might be considered as a formal mistake but should not cause damage for name allocation as all 16 workers and 14 gynes investigated by the first author from the MHN Genève collection were consistent and represented a single species. We refer here as unambiguous type material three workers on the same pin labelled "Typus" [red printed label], "Tapinoma erraticum Ltr.var.madeirense Forel, Ribeira Brava, Madeira" [handwritten], "Coll. A. Forel" [printed], depository MHN Genève. We also recognize as types three gynes (one beheaded) on the same pin, labelled "Typus" [red label], "Tapinoma erraticum Latr. var.madeirense Forel, Ribeira Brava, Madeira" [handwritten], "Coll A.Forel", "LECTOTYPE Tapinoma erraticum var. madeirense Forel desig. Wetterer & Espadaler" [printed label]; depository MHN Genève. Investigated from the MNH Genève collection were furthermore 13 workers and 11 gynes collected by Schmitz in Madeira.

*Tapinoma erraticum ssp. ambiguum* Emery 1925 [type investigation]
The taxon has been described from Departement Drôme (France), New Forest (England) and Prague (Czechia). All this material was available from MCSN Genova and consisted of three different species. A lectotype has been fixed by Seifert (2012) in a male, labelled "Drôme France Forel ♂", "SYNTYPUS Tapinoma erraticum subsp. ambiguum Emery, 1925", "T. erraticum ambiguum" and "Lectotype Tapinoma ambiguum Emery, 1925 design. B.Seifert 2010". A wild-card run of the lectotype in a LDA using ML and the genital characters SPExc, SPdT, SPWPR, dSPST allocated the lectotype with p= 0.9796 to the *T. madeirens*e cluster (see below). Among four paralectotype workers from Czechia labelled "Prag Wasmann", "SYNTYPUS Tapinoma erraticum subsp. ambiguum Emery, 1925", one specimen belonged to *T. subboreale* (*T. madeirense* is excluded by geographic indication) whereas the other three specimens belonged to *T. erraticum* with p > 0.999, using 15 NUMOBAT characters).

**Material examined**. Considering also samples with very weak separation from the sibling species *T. subboreale*, numeric phenotypical data were taken in workers in 22 samples with 78 individuals. They originated from Austria (1 sample), France (4), Italy (4), Portugal (8), and Spain (5). For details see supplementary information SI1, SI2.

The more safely separable males were investigated in 9 samples with 25 individuals. They originated from France (7 samples) and Portugal (2). For details see supplementary information SI3.

**Geographic range**. Considering samples with sufficiently safe morphological and/or genetic indication, *T. madeirense* is by natural distribution a Westmediterranean species found in Madeira ( 17.0°W, 32,5°N), the whole Iberian Peninsula and S France north to 44.2°N. Nests found in a sealed area with some greenery in the city of Sanremo (43.820°N, 7.787°E) and in a grassland patch in a commercial zone in the city of Parma (44.787°N, 10.381°E) could represent anthropogenous introductions to Italy. The latter is sure for a finding in an apartment house in the city center of Vienna (48.182°N, 16.360°E). *T. madeirense* goes up to 1280 m in Spain at 37.3 °N.

**Diagnosis**:—Worker (Tab. 2, Figs. 30–32): All shape ratios given below are, in contrast to those in Tab. 2, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Rather small, CS 694 ± 63 μm. Head moderately elongated CL/CW 1.153 ± 0.040. Postocular distance medium-sized, PoOc/CL 0.419 ± 0.009. Anteromedian clypeal excision shallow and wider than deep, ExCly/CS 4.73 ± 0.66 %, ExClyW 6.48 ± 0.90%. The margin of clypeal excision forms a sharp cuticular edge and is at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few micron across margin of clypeal excision low, nExCly 1.87 ± 0.65. Posterior margin of head in full face view not excavated, ExOcc/CS 0.15 ± 0.19 %. Scape moderately elongated, SL/CS 1.022 ± 0.018. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN/CS 0.291 ± 0.007. Eye rather large, EL/CS 0.280 ± 0.007. Metanotal groove rather shallow, MGr/CS 3.08 ± 0.97 %. Mesosoma relatively wide and long, MW/CS 0.661 ± 0.024, ML/CS 1.344 ± 0.028. Second funiculus segment short, Fu2L/CS 12.81 ± 0.47%, IFu2 1.451 ± 0.085. Head, mesosoma and gaster covered by a rather dense pubescence. Anterior margin of clypeus with a few standing setae, the two longest and strongest are based near to the anterolateral margin of clypeal excision. Remaining surface of head capsule and dorsal mesosoma without standing setae, such are present on mandibles, coxae and ventral surface of gaster. Head, mesosoma and gaster dark blackish brown. Antennae, femora and tibia dark brown. Tarsae and metatarsae usually pale yellowish brown.

—Male genital (Tab. 6, Fig. 33): Tips of subgenital plate less distant and depth of excision of subgenital plate much lower than in *T. subboreale*, SPdT/ML 0.313 ±0.031, SPExc/ML 0.167 ±0.019. Longitudinal distance of the tips of subgenital plate and the tips of the harpago much larger than in *T. subboreale*, dSPST/ML 0.145 ±0.019.

**Taxonomic comments.** The taxonomic separation of *T. madeirense* and *subboreale* is maintained here despite difficulties to separate the female castes morphologically. The decision is based on successful classification based on male genital characters and support of these classifications by microsatellite data. As overall picture, the nuDNA data indicated an Iberian glacial refuge in *madeirense* and an Italo-Balkanian refuge in *subboreale* (Fig. 51) and some introgression in the contact zone in southern France (Fig. 53). Sample means of males could be fully separated by the exploratory data analyses NC-Ward, NC-part.kmeans and NC-NMDS.kmeans using the absolute measurements ML, SPExc, SPdT, SPWPr and dSPST. These classifications were confirmed by a PCA and LDA in any of the 32 nest samples (Fig. 52) and in 98% of 102 Individuals (all raw data are given in supplementary information SI3).

In contrast to these clear results, no exploratory data analysis run with NUMOBAT data of worker samples provided a reasonable species hypothesis. The only approach was here to run a LDA with hypotheses being pre-established in those 50 samples having a credible classification by associated males or by a clear geographic or genetic indication whereas the remaining 17 samples were run as wild-cards. Finally, within a total of 67 samples, only 43% could be classified with posterior probabilities of p > 0.90. This indicates the weak performance of the selected NUMOBAT characters in this case.

The rather clear west-east population separation shown by nuDNA with an Iberian glacial refuge for *madeirense* and an Italo-Balkanian one for *subboreale* requires additional comments. *T. madeirense* arrived in Mediterranean S France probably before *subboreale*, using the coastal route from Spain alongside other ant species such as *Lasius cinereus* Seifert 1992 or *Cataglyphis piliscapa* Forel 1901. Investigation of nuDNA data in Southern France in localities where anthropogenous introduction was unlikely provided a clear signal for ongoing hybridization between *T. madeirense* and *subboreale* (Fig. 53). F1 hybrids or individuals suspected for introgression occurred only in a 50 km long zone along the Rhône river from Nîmes to Montélimar. The establishment of a hybrid zone at the border between Mediterranean and continental bioregions indicates a longstanding equilibrium with *T. subboreale*, with a probable climatic advantage for the more southern *T .madeirense* over *T. subboreale* in the south of this very strong climatic gradient. A recent disturbance of the clear geographic pattern is best explained by anthropogenous introduction. This was obviously the case in findings of *subboreale* (of Italian origins based on microsatellite data)

in several gardening centers and public parks in the Montpellier region or in a finding of *madeirense* in an apartment house in Vienna/Austria. The classification of the latter finding was based on a posterior probability in a wild-card run of a LDA (p=0.9860) but this is no really sure indication considering the weak performance of the character system. Whatever is true, *Tapinoma madeirense* has not to be included in the list of Austrian ants as there is no evidence for outdoor nesting and successful colonization.

**Biology** (according to observations of L. Fraysse from Southern France): Along the French Mediterranean coast and within the Rhône Valley, *T. madeirense* appears to occupy moderately sun exposed places, dry to moist. Nest were found directly in the ground, under stones, or even under little wood pieces in diverse habitats: clear pine forest both with or without dense grass cover, along shaded grassy paths, in suburban gardens, even in a watered truffle oak grove. Centanni *et al* (2022)., based on 100 nests, found that the species was as frequent in semi-natural, agricultural or urban landscapes in and around Montpellier (France). When the nest was directly in the ground, the ants constructed solaria in which the brood is placed just under the surface, using wet soil and the surrounding grasses as it was described for *T. subboreale* and *T. erraticum*. Nest density seems to be relatively low compared to the latter, maybe because desirable habitats are more discontinuous in S France. All colonies in S France contained at most a thousand workers, that are not aggressive when disturbed. Polygyny seems occasional, mature colonies contained 1 to 5 queens. Alates seem to be produced continuously during 2–3 weeks in April or May, depending on the annual climate. Nuptial flights occur at most a week after their emergence, a few alates are emitted regularly during hot mornings. Males were observed to practice a particular strategy: they fly near the ground, land and run for 10–50 cm, and then take off again. Moreover, in swimming pools, only males were found during 6 years of nuptial flight. Hence, it seems that flight dispersal of gynes is weak and that gene flow between populations is largely male-mediated. Workers forage individually for dead little invertebrates, but are very efficient mass recruiters when a sugar source is found (e.g. hemipteran honeydew, fruit peelings in compost etc.). Nests are often translocated within a season—probably to avoid overheating and desiccation or to be closer to sustainable food sources.
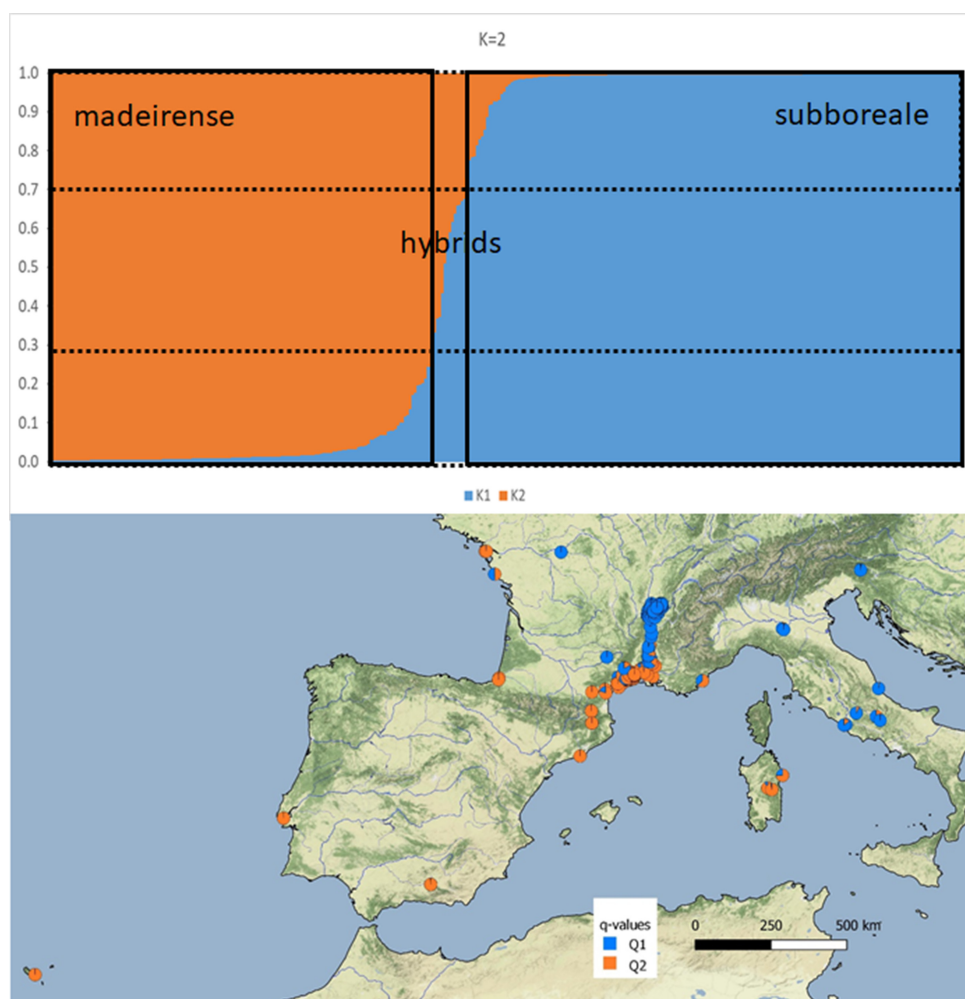


**FIGURE 51.** Bayesian clustering for K=2 of 15 microsatellite loci of *Tapinoma madeirense* (orange) and *T. subboreale* (blue).
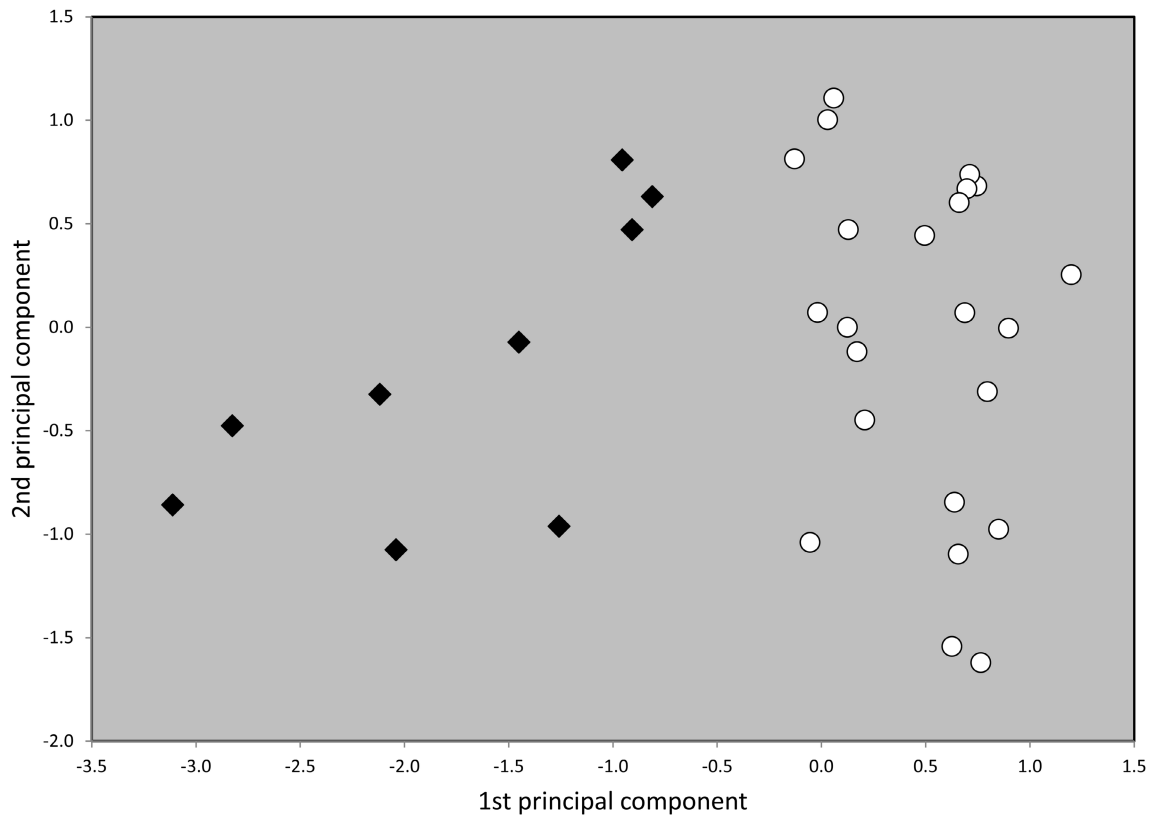
**FIGURE 52.** Separation of nest sample means of males of *Tapinoma madeirense* (black rhombs) and *T. subboreale* (white dots) by a principal component analysis considering 5 NUMOBAT characters.
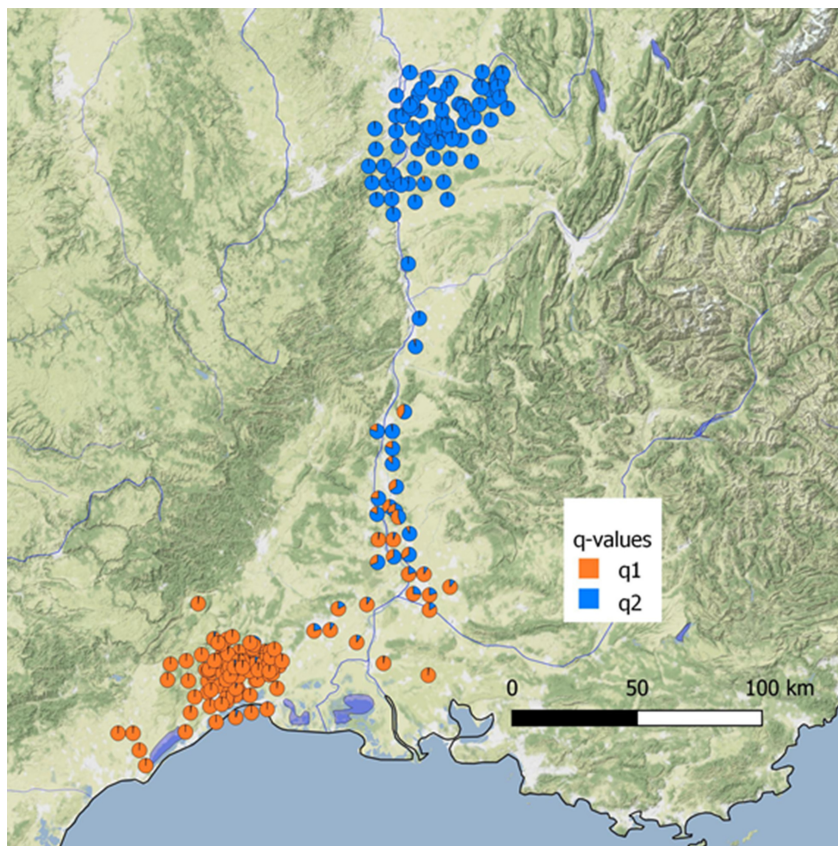


**FIGURE 53.** Bayesian clustering for K=2 of 15 microsatellite loci of *Tapinoma madeirense* (orange) and *T. subboreale* (blue) in southern France with hybridization in a 100 km wide zone along the Rhone river from about Nîmes to Montélimar.

***Tapinoma subboreale*** Seifert 2011

*Tapinoma subboreale* Seifert 2011 [type investigation]

The species was described from Germany. Investigated were the holotype male labelled "GER: 51.2294 °N, 11.7329°E, Weischütz-Kirche 1.7 km NE, limestone grassland, 215 m, Seifert 2002.06.14-542", "Holotype *Tapinoma subboreale* Seifert"; five paratype males and five paratype workers with the same locality label and "Paratype *Tapinoma subboreale* Seifert" on a separate pin (1 male, 2 workers) and in ethanol (4 males, 3 workers); all material from the same nest sample; five paratype gynes labelled "GER: 50.879°N, 10.840°E, 300 m, Wanderlebener Gleiche, B. Seifert 1984.09.03" and "Paratype *Tapinoma subboreale* Seifert"; all material deposited in SMN Görlitz. A wild card run in a LDA using the characters ML, SPExc, SPdT, SPWPR, dSPST allocated the holotype with p= 0.9996 to the *T. subboreale* cluster (see above). The paratype workers from the holotype nest were allocated with p=0.947 to the *T. subboreale* cluster.

**Material examined**. Considering also samples with weak separation from the sibling species *T. madeirense*, numeric phenotypical data were taken in workers in 45 samples with 110 individuals. They originated from Bosnia (1 sample), Bulgaria (1), Croatia (2), Czechia (1), France (6), England (2), Germany (18) Hungary (1), Italy (8), Slovakia (1), Sweden (3) and Ukraine (1). For details see supplementary information SI1, SI2. Males were investigated in 23 samples with 77 individuals. They originated from France (15 samples), Germany (5), Italy (1) and Sweden (2). For details see supplementary information SI3.

**Geographic range**. Considering the available vouchers with sufficiently safe morphological and/or genetic indication, the natural range should include South England (50.65°N, 1.97°W), France, South Sweden (Öland and Gotland, 57.5°N), Central Europe, Italy (here south to 40°N), the Balkans and the Ukraine (49.42°N, 32.06°E). The glacial refuge centers of *T. subboreale* were most probably situated in the Balkans and the Apennine Peninsula. During postglacial spreading it moved west to south France from where it went north to West Germany, South England and South Sweden. East Austria, East Germany and Poland were certainly colonized from the Balkans via the route over the Hungarian plain. Recent findings of *T. subboreale* within the range of *T. madeirense* in several gardening centers and public parks in the Montpellier region should represent introductions from Italy which is suggested by habitat, microsatellite data and mtDNA haplotype sharing with Italian samples. Near the southern distributional border (41.9°N) *T. subboreale* goes up to 1600 m.

**Diagnosis**:—Worker (Tab. 2): All shape ratios given below are, in contrast to those in Tab. 2, primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Extremely similar to *T. madeirense*. Slightly larger than the latter, CS 720 ± 71 μm. Head moderately elongated CL/CW 1.145 ± 0.037. Postocular distance medium-sized, PoOc/CL 0.415 ± 0.009. Anteromedian clypeal excision slightly deeper and wider than in *T. madeirense*, ExCly/CS 5.19 ± 0.60 %, ExClyW 7.34 ± 0.82 %. The margin of clypeal excision forms a sharp cuticular edge and is at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few micron across margin of clypeal excision low, nExCly 1.81 ± 0.75. Posterior margin of head in full face view usually not excavated, ExOcc/CS 0.34 ± 0.37 %. Scape moderately elongated, SL/CS 1.019 ± 0.022. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN/CS 0.294 ± 0.007. Eye rather large, EL/CS 0.280 ± 0.007. Metanotal groove slightly deeper than in *T. madeirense*, MGr/CS 3.35 ± 1.02 %. Mesosoma relatively wide and long, MW/CS 0.660 ± 0.021, ML/CS 1.365 ± 0.028. Second funiculus segment slightly longer than in *T. madeirense*, Fu2L/CS 13.12 ± 0.37 %, IFu2 1.472 ± 0.071. Pubescence, seta characters and pigmentation as in *T. madeirense*.

—Male genital (Tab. 6, Fig. 34): Tips of subgenital plate more distant and depth of excision of subgenital plate much larger than in *T. madeirense*, SPdT/ML 0.350 ±0.023, SPExc/ML 0.204 ±0.014. Longitudinal distance of the tips of subgenital plate and of the tips of the harpago much smaller than in *T. madeirense*, dSPST/ML 0.100 ±0.014.

**Taxonomic comments.** The taxonomic relations to the cryptic sister species *T. madeirense* were discussed above. Despite hybridization in a contact zone in southern France, we maintained the specific status of *T. subboreale* because there is, on a larger geographic scale, a sufficient separation by genetics and male genital characters.

**Biology.** For a condensed description see Seifert (2018). Recent field sampling in the French Rhône valley showed that *T. subboreale* is more easily found than *T. madeirense,* as it builds larger solaria and exhibits higher densities in all dry to moist meadows, where it co-occurs with *T. erraticum*. In the transition zone between *T. subboreale* and *T. madeirense*, both species are difficult to find and their favored habitat remains unclear. In a large

ecological study in Central Europe, Seifert (2017) could demonstrate a strong competive exclusion between *T. subboreale* and *T. erraticum* based on the contrast between high overlap of fundamental niche spaces and avoidance of syntopic occurrence in the sympatric range.

## *Tapinoma pygmaeum* (Dufour 1857)

*Micromyrma pygmaea* Dufour 1857 [original description, zoogeography]
The species was described from a garden in Saint-Sever, SW France. The information provided by Dufour's drawings and verbal description on petiole shape, number of funiculus segments and mandibular dentition make clear that it does not belong to the genus *Plagiolepis* but instead represents a tiny *Tapinoma* with very feeble clypeal excavation. Furthermore, outdoor nesting and the climatic situation of the type locality by the middle of the 19th century exclude considering introduced tropical *Tapinoma* species.

**Material examined**. Numeric phenotypical data were taken in 7 samples with 18 workers. They originated from Belgium (2 samples), France (1), Italy (1 sample), Spain (1) and Switzerland (2). For details see supplementary information SI1, SI2.

**Geographic range**. Only 12 outdoor sites are documented so far from Spain, S France, south Switzerland and Italy in a rather small area between 1°E and 9°E, 41°N and 47°N and from close to sea level up to 1944 m.

**Diagnosis**:—Worker (Tab. 7, Figs. 9–11): All shape ratios given below are primary ratios without RAV and all data are given as arithmetic mean ± standard deviation. Tiny size, CS 488 ± 23 μm. Head moderately elongated CL/CW 1.141 ± 0.024. Postocular distance very large, PoOc/CL 0.500 ± 0.007. Anteromedian clypeal excision absent or very shallow, ExCly/CS 0.55 ± 0.34 %, ExClyW 11.76 ± 2.07 %. Sum of pubescence hairs and small setae protruding at a few micron across margin of clypeal excision low, nExCly 0.97 ± 0.92. Posterior margin of head not or only very slightly excavated, ExOcc/CS 1.08 ± 0.49 %. Scape shorter than in any Palaearctic species, SL/CS 0.846 ± 0.019. Minimum distance of the inner margins of antennal socket rings relatively wide, dAN/CS 0.323 ± 0.009. Eye small, EL/CS 0.244 ± 0.006. Metanotal groove shallow, MGr/CS 1.57 ± 0.44 %. Mesosoma relatively narrow and shorter than in any small species, MW/CS 0.624 ± 0.023, ML/CS 1.157 ± 0.028. Second funiculus segment extremely short, shorter than in any Palaearctic species, Fu2L/CS 8.28 ± 0.39 %, IFu2 0.933 ± 0.057. Head, mesosoma and gaster dark brown. Antennae, femora and tibiae, metatarsae and tarsae medium brown to pale yellowish brown. Condition of pubescence without species-specific characters. Anteromedian clypeal margin with four conspicuous setae which are much longer than other setae on whole body.

—Male genital: See the drawing and description provided by Espadaler (1978).

**Taxonomic comments.** *Tapinoma pygmaeum* can not be confused with any Palaearctic species with outdoor occurrence. The very small size, the very large postocular index, the extremely short second funiculus segment and scape suggest proximity to species related to *Tapinoma melanocephalum* (Fabricius 1793). There is indeed a high morphometric similarity to the recently described tropical *Tapinoma pithecorum* Seifert 2022 which occurrence in the temperate zone is restricted to heated greenhouses. *Tapinoma pithecorum* differs from *T. pygmaeum* by a whitish gaster pigmentation contrasting the blackish brown mesosoma, by a broader mesosoma and an even shorter 2nd funiculus segment. Using absolute measurements given in mm, the two species can be separated by a discriminan 92.69*PoOc+344.0*ExCly+374.2*Fu2L−73.02*MW−16.08 with 14 workers of *pithecorum* showing values < 0 and 18 workers of *pygmaeum* values > 0.

**Biology.** According to Espadaler & Garcia-Berthou (1997) and Espadaler (pers. comm. 2023), it is often found in habitats with certain degree of humidity as it occurred in a mixed forest along water courses, at a margin of a lake or frequently on mountain meadows. Occurrence in city parks (Ruiz-Heraz *et al.* 2011) and gardens shows that it does not avoid habitats with stronger anthropogenic disturbance. Altitudinal distribution and habitat type indicate that thermophily during the summer season is not very expressed and that nests are relatively frost resistant. In the region of its natural origin it is a comparatively rare and unspectacular ant but was certainly underrecorded in the past because collectors in the field were not alerted due to superficial similarity with tiny *Plagiolepis* species. Nests were found under stones, in rock crevices, in dead dry wood, in the stem of an old vine and of a *Rubus* plant and even in the pit of a peach still hanging on the tree. The nest habitats of two findings from the Canton of Vaud, Switzerland were an active bee hive and an unheated glasshouse of a private house. Lebas *et al.* (2016) reported French colonies to contain not more than 100 workers and to frequently translocate nest sites to have better access to food sources.

Espadaler (pers. comm. 2023) estimated the population under a flat stone to consist of > 10 queens and likely 300–400 without making digging attempts to enumerate the full population. In the altitudinal range of 1400 to 1500 m of the El Catllar mountain area / East Pyrenees, sexuals were observed by Espadaler 2 July 1977 and 18 July 2018. The introduced population in a glasshouse in Eeklo, Belgium is of particular interest as it was very polygynous and populous and foraged in the garden. We probably witness here the transition to supercoloniality in an introduction site of a species which is not known to be a pest species in the region of its natural origin. Considering global warming, nests of *Tapinoma pygmaeum* introduced to England and the Benelux countries should be well able to survive there the winters in outdoor habitats. Frost resistance is indicated by frequent occurrence in the El Catllar region between 1150 and 1944 m which corresponds to mean January temperatures between +1°C and -4°C.


## *Tapinoma kinburni* Karavaiev 1937

*Tapinoma kinburni* Karavaiev 1937 [image of neotype, topotypical specimens]
The species was described from Zolonoozerna Dacha (46.462°N, 32.159°E, 3 m), 6 km W of Rybalche, Kinburn penisula, Ukraine. The diagnosis presented here is based on investigation of the image CASENT0917470 of the neotype and of three worker series from the type locality.

**Material examined**. Numeric phenotypical data were taken in 3 samples with 7 workers. They originated from the type locality in the Ukraine. For details see supplementary information SI1, SI2.

**Geographic range**. So far only known from the type locality and a site near to the Korsun Monastery (46.76°N, 33.19°E).

**Diagnosis**:—Worker (Tab. 7, Figs. 21–23): All shape ratios given below are primary ratios without RAV and all data are given as arithmetic mean ± standard deviation (n-weighted). Small size, CS 586 ± 24 μm. Head moderately elongated CL/CW 1.137 ± 0.024. Postocular distance medium-sized, PoOc/CL 0.435 ± 0.008. Anteromedian clypeal excision shallow and broad, ExCly/CS 2.96 ± 0.30 %, ExClyW 8.12 ± 0.84 %. Pubescence hairs and fine setae protruding at a few micron across margin of clypeal excision usually absent, nExCly 0.43 ± 0.53; clypeus margin lateral of the excision with 3–5 long and 3–4 shorter setae. Posterior margin of head not or only very slightly excavated, ExOcc/CS 0.73 ± 0.47 %. Scape short, SL/CS 0.24 ± 0.013. Second funiculus segment very short, Fu2L/CS 10.18 ± 0.35 %, IFu2 1.141 ± 0.068. Minimum distance of the inner margins of antennal socket medium-sized, dAN/CS 0.303 ± 0.005. Eye moderately large, EL/CS 0.273 ± 0.006. Mesosoma relatively narrow and rather short, MW/CS 0.631 ± 0.011, ML/CS 1.219 ± 0.036. Metanotal depression rather shallow, MGr/CS 2.47 ± 0.38 %. Whole body homogeneously dark to blackish brown; metatarsae, tarsae, distal end of scape and often mandible pale yellowish brown.

—Male genital: see drawings in Radchenko (1983).

**Taxonomic comments.** As a combination of small size, short scape and second funiculus segment, and shallow clypeal excision not to confuse. Nanitic workers of *Tapinoma subboreale*, which have a similar body size, can be distinguished by SL/CS > 0.970 and Fu2L/CS > 0.117.

**Biology** [according to Karavaiev (1937) and Radchenko (1983)]. The findings were made in semi-open sandy areas covered by xerophile plants and interspersed with small salt lakes and stands of arboreal relict flora such as Pedunculate Oak and Silver Birch. The nests are in soil, in patches with incomplete turf cover and have entrance holes of 2–4 mm diameter which are often surrounded by crater-like sand ejections of up to 8 cm diameter. Foraging is diurnal and only interrupted during the hottest post-meridiem hours. Alates were observed between 16 June and 20 July.


## *Tapinoma sinense* Emery 1925

*Tapinoma sinense* Emery 1925 [evaluation of image of type]
The species has been described based on material collected by Zichy in Mongolia. The diagnosis is based on evaluation of the image CASENT0904016 in ww.antweb.org of a type worker labelled ""T. sinense Emery", "Mongolia Burgaltai", "Exp. Zichy leg. Csiki", "IX.5.1898.", "TYPUS", "ANTWEB CASENT0904016".

*Tapinoma emeryanum* Kuznetzov-Ugamsky 1927 [evaluation of images of types]

This taxon has been described from two localities in the W Tian Shan region. Investigated were the images of a type worker (CASENT0911577 in www.antweb.org) labelled "West. Tian-Shan Ak-Tasch. 2400 m. Kuznezow", "Tapinoma emeryana Ku", "Type", "Sammlung Dr. F. Santschi Kairouan", "ANTWEB CASENT0911577" and images of a syntype worker (CASENT0917850 in www.antweb.org) labelled "..Tamerlanovka ..Bugunja...26/ VI -23", "Syntypus Tapinoma emeryanum Kuzn.", "N 460 3-0-0" and "ANTWEB CASENT0917850".

Scatterplots of CL, CW, PoOc, SL, ML and dAN indicate synonymy of *Tapinoma emeryanum* with *T. sinense* and a wide distance from other species with shallow clypeal excision.

**Material examined**. Only images of three type specimens from Kazakhstan, Kyrgistan and Mongolia were available.

**Geographic range**. Tamerlanovka (42.59° N, 69.26° E, 290 m), Ak Tash (41.2° N, 70.6° E, 2400 m), Burgaltay (49.265° N, 104.743° E, 1020 m).

**Diagnosis**:—Worker (Tab. 7, Figs. 12, 13): All shape ratios given below are primary ratios without RAV and all data are given as arithmetic mean ± standard deviation (n-weighted). Rather small, CS 673 ± 40 μm. Head very short, CL/CW 1.057 ± 0.035. Postocular distance large, PoOc/CL 0.444 ± 0.006. Anteromedian clypeal excision very shallow and very broad, ExCly/CS 2.76 ± 0.45 %, ExClyW 10.16 ± 1.52 %. Few pubescence hairs and small setae protruding a few micron across margin of clypeal excision, nExCly 2.33 ± 0.47. Posterior margin of head very slightly excavated, ExOcc/CS 0.74 ± 0.20 %. Scape very short, SL/CS 0.903 ± 0.012. Second funiculus segment short, Fu2L/CS 11.12 ± 0.04 %, IFu2 1.225 ± 0.091. Minimum distance of the inner margins of antennal socket rings moderate, dAN/CS 0.314 ± 0.010. Eye medium-sized, EL/CS 0.285 ± 0.011. Mesosoma moderately wide and short, MW/CS 0.650 ± 0.033, ML/CS 1.191 ± 0.015. Metanotal depression rather shallow, MGr/CS 2.94 ± 0.82 %. Color of head, mesosoma and gaster dirty brown, mandibles femora, tibiae, metatarsae and tarsae paler.

**Taxonomic comments.** As a combination of very shallow clypeal excision, small CL/CW, small SL/CS, small ML/CS and large PoOc/CL, the species is not to confuse with any known species from Central and East Asia (Tab. 7).

**Biology.** Sexuals were found in the Tian Shan 29 July 1922.


## *Tapinoma christophi* Emery 1925

*Tapinoma christophi* Emery 1925 [type investigation]

The species has been described only on the base of males collected by Christoph at Sarepta (48.512°N, 44.550°E) south of Volgograd. Investigated were two syntype males (one without gaster) labelled "Sarepta Christoph", "T. christophi Emery" [both in Emery's handwriting], "ANTWEB CASENT 0904025", "SYNTYPUS Tapinoma christophi Emery, 1925". Depository MCSN Genova.

**Geographic range**. Only known from the type locality.

**Taxonomic comments.** *Tapinoma christophi* is considered here as a valid species because the undamaged syntype male shows a number of extreme characters which exclude a synonymy with any species in which males are known. It is a combination of rather small size (CS=764 μm), extremely short scape (SL/CS 0.948), short head (CL/CW 0.847) and very shallow clypeal excision (ExCly/CS 1.81%). The genital is also unusual. In ventral view, the caudal ends of the basimeres are semicircular and do not surpass the apices of the subgenital plate. The tips of harpago surpass the tips of the subgenital plate by a distance nearly equal to the depth of the excision of the subgenital plate. Considering the extreme data of head characters and that we have correlation of male and female characters in *Tapinoma*, *T. christophi* might be related to *T. sinense* the workers of which are likewise a combination of rather small size, extremely short scape, short head and very shallow clypeal excision (Tab. 7). The question if *christophi* might be a synonym of *sinense* cannot be answered in reasonably short time and will probably require the study of variation in sufficiently large male material of both taxa.

**Biology.** Unknown.

## *Tapinoma dabashanica* n.sp.

Etymology: referring to the mountain range Daba Shan where the type sample was collected.

**Type material:** Holotype plus 2 paratype worker on the same pin labeled "China Chongging Dabashan MtR S Gaoguan N 31.819 E 108.902 1590 m asl 2010-05-18 Belousov Kabak & Korolev Chi 2010 182b"; depository SMN Görlitz.

**Geographic range**. Only known from the type locality.

**Diagnosis**:—Worker (Tab. 7, Figs. 14-16): All shape ratios given below are given in the sequence arithmetic mean [minimum, maximum]. Small-sized, CS 650 [628, 665]. Head elongated CL/CW 1.160 [1.147, 1.182]. Postocular distance medium-sized, PoOc/CL 0.411 [0.409, 0.413]. Anteromedian clypeal excision wider than deep, ExCly/CS 4.38 [4.25, 4.58]%, ExClyW 8.38 [8.11, 8.82]%. The margin of clypeal excision forms a sharp cuticular edge being at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few micron across margin of clypeal excision low, nExCly 3.67 [3.0, 4.0]. Posterior margin of head in full face view not excavated, ExOcc/CS 0.0 [0.0, 0.0]%. Scape moderately elongated, SL/CS 0.991 [0.987, 0.994]. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN 0.300 [0.297, 0.304]. Eye rather long, EL/CS 0.298 [0.295, 0.303]. Dorsal profile of mesonotum and of propodeum more strongly convex, metanotal depression rather deep, MGr/CS 2.57 [1.79, 3.62]%. Mesosoma relatively thickset, MW/CS 0.682 [0.658, 0.704], ML/CS 1.293 [1.263, 1.315]. Second funiculus segment short, Fu2L/CS 12.79 [12.60, 12.91]%, IFu2 1.357 [1.333, 1.380]. Head, mesosoma and gaster covered by a rather dense pubescence. Anterior margin of clypeus with few short standing setae. Remaining surface of head capsule and dorsal mesosoma without standing setae, such are present on mandibles and coxae. Head, mesosoma, gaster, antennal scape, femora and tibiae dark brown. Tarsae, metatarsae and funiculus segments pale yellowish brown.

**Taxonomic comments.** For separation from the related species *Tapinoma sichuense* **n. sp.** see next chapter.

**Biology.** Unknown.


## *Tapinoma sichuense* n.sp.

Etymology: referring to the Chinese province Sichuan where the two type samples were collected.

**Type material:** Holotype plus 2 paratype worker on the same pin labeled "China, Sichuan, NW Jiuxiangzhen N 29.533, E 102.463, 1310 m asl., 2009-07-08, leg. Kabak, Chi 2009 242a"; 1 paratype worker labelled "CHI: 30.667°N, 100.758°E, Sichuan W. Qiaoqi 3 km S. 1950 m. 1997-07-11", both samples deposited in SMN Görlitz.

**Geographic range**. Only known from the two type localities.

**Diagnosis**:—Worker (Tab. 7 Figs. 17–19): All shape ratios given below are given in the sequence arithmetic mean [minimum, maximum]. Small-sized, CS 695 [665, 720]. Head less elongated than in *dabashanica* **n. sp.**, CL/CW 1.140 [1.126, 1.157]. Postocular rather small, PoOc/CL 0.397 [0.387, 0.404]. Anteromedian clypeal excision wider than deep, ExCly/CS 4.84 [4.69, 5.01]%, ExClyW 7.98 [7.51, 8.75]%. The margin of clypeal excision forms a sharp cuticular edge being at same level as the adjacent clypeal surface. Sum of pubescence hairs and smaller setae protruding at a few micron across margin of clypeal excision low, nExCly 2.0 [2.0, 2.0]. Posterior margin of head in full face view very feebly excavated, ExOcc/CS 0.50 [0.20, 0.77]%. Scape more elongated than in *dabashanica* **n. sp.**, SL/CS 1.040 [1.004, 1.065]. Minimum distance of the inner margins of antennal socket rings medium-sized, dAN 0.305 [0.296, 0.309]. Eye rather large, EL/CS 0.284 [0.279, 0.289]. Dorsal profiles of mesonotum and of propodeum less convex than in *dabashanica* **n. sp.**, metanotal depression rather shallow, MGr/CS 1.84 [1.29, 2.04]%. Mesosoma more slender than in *dabashanica* **n. sp.**, MW/CS 0.662 [0.657, 0.665], ML/CS 1.377 [1.356, 1.394]. Second funiculus segment short, Fu2L/CS 12.74 [12.57, 12.97]%, IFu2 1.403 [1.313, 1.437]. Head, mesosoma and gaster covered by a rather dense pubescence. Anterior margin of clypeus with few short standing setae. Remaining surface of head capsule and dorsal mesosoma without standing setae, a few of these are present on mandibles, coxae and gaster sternites. Head, mesosoma, gaster, antennal scape, femora and tibiae dark to blackish brown. Tarsae, metatarsae and funiculus segments paler.

**Taxonomic comments.** It might be asked if the heterospecificity of *Tapinoma dabashanica* **n. sp.** and *sichuense* **n. sp.** appears credible considering the few specimens available. An first answer might be given when pooling the data of the 7 specimens of both species. This results in a coefficient of variation of 3.65% in the character ML/CS.

The same coefficient is 2.28 ± 0.27 [1.78, 2.95]% in the 19 remaining Palaearctic species. Hence, considering conspecificity of *Tapinoma dabashanica* **n. sp.** and *sichuense* **n. sp.**, the coefficient of variation in ML/CS would be clearly outside the intraspecific variance known in the genus. Another argument for heterospecificity is the differing mesosomal profile which is not caused by allometric effects because the absolute size of all specimens is very similar (compare Figs. 15 and 18). Furthermore, the mountainous type localities of *T. dabashanica* **n. sp.** and *sichuense* **n. sp.** are 700 km apart and separated by a wide lowland area.

 **Biology.** Unknown.


**Incertae Sedis**

The following taxa have been allocated to the genus *Tapinoma* but a proper classification is impossible due to missing types and insufficient information in the original description.


### *Tapinoma atomum* (Latreille 1798)

*Formica atomus* Latreille 1798
Since Roger (1863), this taxon has been synonymized with *Tapinoma erraticum*—for the last time by Shattuck (1994). An allocation to the genus *Tapinoma* appears reasonable based on the description of petiole scale. However, the remaining descriptory statements of Latreille can be applied to at least two different species expected for the type locality Brive.


### *Formica caerulescens* Losana 1834

This taxon has been described from Piemont / Italy and has been considered by all authors since Mayr (1863) as junior synonym of *Tapinoma erraticum*—for the last time by Radchenko (2016). However, the verbal statement of Losana (1834) "...squama subquadrata, emarginata..." and his drawings of petiole scale and dorsal aspect of the whole ant definitely exclude that it belongs to the genus *Tapinoma*. It is a member of the subfamily Formicinae—most probably either a species of *Lasius* Fabricius 1804 or *Formica* Linnaeus 1758.

## Morphometric tables

**TABLE 2.** RAV-corrected morphometric data of workers of medium-sized *Tapinoma* species with sharp-edged clypeal excision at middle depth level, low number of microsetae at clypeal excision and less elongated 2nd funiculus segment. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

| | *erraticum* (n=131) | *glabrella* (n=219) | *israelis* (n=30) | *festae* (n=30) | *subboreale* (n=112) | *madeirense* (n=69) |
|---|---|---|---|---|---|---|
| CS | 761 ± 89 [593, 974] | 777 ± 83 [600, 1036] | 730 ± 67 [624, 907] | 808 ±95 [656,954] | 719 ±72 [561,874] | 691 ±61 [560,837] |
| CL/CW 0.9 | 1.060 ±0.017 [1.013,1.104] | 1.068 ±0.024 [1.002,1.118] | 1.093 ±0.018 [1.053,1.123] | 0.991 ±0.013 [0.967,1.014] | 1.062 ±0.016 [1.020,1.114] | 1.059 ±0.023 [0.972,1.099] |
| SL/CS 0.9 | 0.987 ±0.018 [0.923,1.046] | 0.962 ±0.020 [0.900,1.030] | 0.981 ±0.014 [0.948,1.016] | 0.970 ±0.014 [0.952,0.997] | 0.982 ±0.019 [0.925,1.025] | 0.976 ±0.018 [0.931,1.014] |
| ExOcc/CS 0.9 [%] | 1.90 ±0.75 [0.33,3.94] | 1.51 ±0.89 [0.00,4.13] | 1.24 ±0.66 [0.20,2.69] | 1.83 ±0.91 [0.37,4.00] | 0.65 ±0.86 [0.00,3.86] | 0.25 ±0.32 [0.00,1.11] |
| ExCly/CS 0.9 [%] | 8.75 ±0.79 [6.19,10.52] | 9.41 ±1.52 [3.05,12.26] | 5.68 ±0.64 [4.27, 7.15] | 3.88 ±0.51 [2.84,5.29] | 5.44 ±0.66 [3.33,7.21] | 5.04 ±0.72 [3.53,6.78] |
| ExClyW/CS 0.9 [%] | 6.44 ±0.63 [4.75, 8.77] | 5.73 ±0.68 [3.65, 7.50] | 5.75 ±0.65 [4.65, 6.72] | 9.11 ±1.99 [6.20,13.68] | 6.91 ±0.87 [5.04,10.44] | 6.25 ±0.85 [3.87,8.18] 49 |
| ExClyL/W 0.9 [%] | 1.37 ±0.17 [0.89,1.87] | 1.66 ±0.36 [0.65,2.94] | 0.99 ±0.10 [0.84,1.21] | 0.44 ±0.10 [0.25,0.63] | 0.79 ±0.09 [0.57,1.04] | 0.78 ±0.10 [0.62,1.04] 49 |
| nExCly 0.9 | 3.13 ±1.59 [0.0, 8.8] | 5.72 ±3.65 [0.0,19.6] | 2.66 ±0.95 [0.0, 5.2] | 3.04 ±1.24 [0.0, 6.1] | 2.41 ±0.98 [0.0,4.9] | 2.68 ±0.96 [0.0,4.6] 49 |
| dAN/CS 0.9 | 0.290 ±0.008 [0.271,0.306] | 0.285 ±0.008 [0.258,0.319] | 0.303 ±0.004 [0.294,0.311] | 0.322 ±0.007 [0.310,0.333] | 0.295 ±0.007 [0.277,0.312] | 0.291 ±0.007 [0.279,0.306] |
| PoOc/CL 0.9 | 0.402 ±0.006 [0.392,0.418] 33 | 0.398 ±0.010 [0.371,0.423] 207 | 0.400 ±0.005 [0.390,0.408] 16 | 0.378 ±0.0011 [0.352,0.395] | 0.405 ±0.007 [0.391,0.423] 36 | 0.407 ±0.008 [0.395,0.429] 22 |
| EL/CS 0.9 | 0.251 ±0.006 [0.237,0.268] | 0.263 ±0.007 [0.245,0.290] | 0.266 ±0.007 [0.255,0.283] | 0.261 ±0.009 [0.249,0.278] | 0.267 ±0.006 [0.249,0.281] | 0.263 ±0.005 [0.250,0.284] |
| MGr/CS 0.9 [%] | 4.46 ±1.01 [2.31,7.84] | 3.52 ±1.05 [0.81,6.75] | 4.88 ±0.88 [3.21,6.44] | 4.25 ±0.86 [3.05,6.53] | 3.99 ±1.04 [1.62,6.45] | 3.75 ±1.12 [0.99,6.16] |
| MW/CS 0.9 | 0.673 ±0.025 [0.623,0.768] | 0.654 ±0.023 [0.589,0.749] | 0.657 ±0.015 [0.632,0.689] | 0.684 ±0.023 [0.646,0.749] | 0.671 ±0.020 [0.635,0.720] | 0.674 ±0.025 [0.630,0.760] |
| ML/CS 0.9 | 1.347 ±0.029 [1.274,1.422] | 1.315 ±0.035 [1.210,1.387] | 1.352 ±0.026 [1.302,1.410] | 1.314±0.029 [1.235,1.361] | 1.354 ±0.028 [1.272,1.408] | 1.331 ±0.029 [1.268,1.394] |
| Fu2L/CS 0.9 [%] | 14.21 ±0.39 [13.20,15.37] | 13.35 ±0.40 [12.01,14.49] | 14.08 ±0.35 [13.22,14.79] | 12.42 ±0.22 [11.89,12.85] | 13.02 ±0.38 [11.81,14.13] | 12.64 ±0.48 [11.61,13.75] 49 |
| IFu2 0.9 | 1.705 ±0.056 [1.569,1.901] | 1.639 ±0.067 [1.408,1.845] | 1.716 ±0.050 [1.600,1.797] | 1.497 ±0.072 [1.229,1.571] | 1.559 ±0.064 [1.380,1.710] | 1.537 ±0.068 [1.389,1.686] 49 |

**TABLE 3.** RAV-corrected morphometric data of workers of the *Tapinoma nigerrimum* group—large-sized species with blunt-edged clypeal excision, high number of microsetae at clypeal excision and much elongated 2nd funiculus segment. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

| | *darioi* (n=210) | *ibericum* (n=211) | *magnum* (n=387) | *nigerrimum* (n=73) | *hispanicum* n.sp. (n=88) |
|---|---|---|---|---|---|
| CS | 897 ± 134 [609, 1157] | 977 ±165 [660,1326] | 965 ±146 [646,1293] | 1029 ±193 [623,1330] | 920 ±143 [628,1266] |
| CL/CW 0.9 | 1.043 ±0.020 [0.960,1.105] | 1.051 ±0.019 [0.999,1.114] | 1.063 ±0.019 [1.008,1.135] | 1.037 ±0.017 [0.967,1.077] | 1.032 ±0.015 [1.005,1.081] |
| SL/CS 0.9 | 0.967 ±0.017 [0.919,1.010] | 0.971 ±0.018 [0.919,1.019] | 0.987 ±0.018 [0.929,1.053] | 0.964 ±0.014 [0.928,1.006] | 0.932 ±0.016 [0.901,0.980] |
| ExOcc/CS 0.9 [%] | 2.08 ±0.73 [0.22,5.51] | 1.86 ±0.62 [0.14,3.77] | 1.48 ±0.59 [0.00,3.34] | 2.19 ±0.55 [0.95,3.87] | 2.17 ±0.67 [0.97,4.19] |
| ExCly/CS 0.9 [%] | 9.93 ±0.90 [7.24,14.61] | 10.61 ±0.77 [6.66,12.49] | 8.91 ±1.01 [4.50,11.44] | 10.17 ±0.88 [6.84,13.87] | 10.71 ±0.92 [7.42,12.96] |
| ExClyW/CS 0.9 [%] | 6.14 ±0.74 [4.08, 8.16] | 6.60 ±0.74 [4.31, 8.48] | 6.84 ±0.74 [4.97, 9.13] | 6.84 ±0.65 [5.95,10.02] | 6.93 ±0.66 [4.35, 8.64] |
| ExClyL/W 0.9 [%] | 1.64 ±0.25 [1.11,2.62] | 1.62 ±0.21 [1.05,2.44] | 1.34 ±0.19 [0.73,2.09] | 1.49 ±0.20 [0.86,2.24] | 1.55 ±0.17 [0.97,2.16] |
| nExCly 0.9 | 14.1 ±4.2 [4.4,25.1] | 16.4 ±4.9 [4.4,30.5] | 13.5 ±4.2 [1.5,24.9] | 13.6 ±4.1 [4.9,23.3] | 17.1 ±4.6 [5.5,25.7] |
| dAN/CS 0.9 | 0.300 ±0.007 [0.283,0.326] | 0.292 ±0.006 [0.274,0.314] | 0.310 ±0.008 [0.288,0.336] | 0.302 ±0.006 [0.290,0.314] | 0.300 ±0.007 [0.284,0.319] |
| PoOc/CL 0.9 | 0.375 ±0.010 [0.346,0.425] | 0.369 ±0.010 [0.334,0.395] | 0.370 ±0.011 [0.341,0.395] 210 | 0.376 ±0.010 [0.349,0.398] 44 | 0.382 ±0.010 [0.350,0.408] |
| EL/CS 0.9 | 0.253 ±0.007 [0.231,0.270] | 0.255 ±0.008 [0.237,0.280] | 0.261 ±0.007 [0.237,0.289] | 0.236 ±0.006 [0.221,0.250] | 0.231 ±0.007 [0.212,0.247] |
| MGr/CS 0.9 [%] | 2.76 ±0.64 [1.20,4.67] | 2.95 ±0.59 [1.01,5.21] | 3.89 ±0.68 [1.25,6.59] | 3.56 ±0.55 [2.40,4.79] | 2.69 ±0.64 [1.16,4.11] |
| MW/CS 0.9 | 0.633 ±0.020 [0.587,0.699] | 0.628 ±0.019 [0.583,0.695] | 0.642 ±0.018 [0.600,0.711] | 0.615 ±0.013 [0.589,0.647] | 0.614 ±0.015 [0.578,0.649] |
| ML/CS 0.9 | 1.277 ±0.028 [1.212,1.362] | 1.284 ±0.030 [1.218,1.385] | 1.300 ±0.030 [1.221,1.419] | 1.238 ±0.021 [1.197,1.300] | 1.224 ±0.027 [1.168,1.289] |
| Fu2L/CS 0.9 [%] | 14.57 ±0.42 [13.56,15.92] | 14.35 ±0.49 [12.71,15.51] | 14.97 ±0.42 [13.52,16.51] | 13.81 ±0.28 [13.10,14.40] | 13.77 ±0.38 [12.93,14.98] |
| IFu2 0.9 | 1.977 ±0.069 [1.812,2.225] | 1.885 ±0.070 [1.596,2.074] | 1.917 ±0.075 [1.660,2.138] | 1.812 ±0.053 [1.715,1.946] | 1.835 ±0.062 [1.657,2.006] |

**TABLE 4.** Posterior probabilities in wild-card runs of a LDA of the three *Tapinoma nigerrimum* group samples with disagreeing NUMOBAT and nuDNA classification as belonging to either *T. darioi*, *T. hispanicum* **n. sp.** and *T. ibericum*. The morphological classification used 15 NUMOBAT characters whereas the genetic classification considered the first 3 principal components extracted from microsatellite data.

| | NUMOBAT | | | nuDNA | | |
|---|---|---|---|---|---|---|
| sample | p(dari) | p(hisp) | p(iber) | p(dari) | p(hisp) | p(iber) |
| SPA:Malaga-20190329 | **0.608** | 0.000 | 0.392 | 0.000 | **0.791** | 0.209 |
| NET:Rotterdam-20170315 | 0.004 | 0.000 | **0.996** | 0.007 | **0.790** | 0.203 |
| SPA: Lona d. l. Panaderos-2020925-nest1 | 0.000 | **1.000** | 0.000 | **0.824** | 0.171 | 0.005 |

**TABLE 5.** RAV-corrected morphometric data of workers of the *Tapinoma simrothi* group—rather large-sized species with blunt-edged but narrow clypeal excision, medium number of microsetae at clypeal excision and less elongated 2nd funiculus segment. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum].

| | *karavajevi* (n=121) | *phoeniceum* (n=87) | *simrothi* (n=121) | *insularis* (n=87) |
|---|---|---|---|---|
| CS | 884 ± 96 [646, 1106] | 860 ±84 [656,1046] | 870 ± 94 [634, 1054] | 817 ± 76 [644, 984] |
| CL/CW 0.9 | 1.065 ±0.017 [1.024,1.105] | 1.077 ±0.024 [1.019,1.127] | 1.078 ±0.020 [1.027,1.131] | 1.082 ±0.021 [1.000,1.127] |
| SL/CS 0.9 | 0.971 ±0.016 [0.928,1.009] | 0.964 ±0.026 [0.882,1.021] | 0.956 ±0.017 [0.909,0.994] | 0.937 ±0.019 [0.891,0.979] |
| ExOcc/CS 0.9 [%] | 0.91 ±0.55 [0.00,2.66] | 1.33 ±0.79 [0.00,4.21] | 1.56 ±0.69 [0.09,3.72] | 1.32 ±0.50 [0.17,2.66] |
| ExCly/CS 0.9 [%] | 11.07 ±0.69 [ 8.71,12.64] | 10.78 ±0.98 [ 7.95,13.65] | 12.97 ±0.79 [10.10,15.16] | 11.48 ±0.84 [ 8.84,13.68] |
| ExClyW/CS 0.9 [%] | 5.99 ±0.71 [4.20, 7.88] | 5.12 ±0.63 [3.38, 6.76] | 5.98 ±0.80 [3.57, 8.93] | 5.33 ±0.70 [3.99, 7.44] |
| ExClyL/W 0.9 [%] | 1.87 ±0.28 [1.40,3.00] | 2.13 ±0.34 [1.58,3.61] | 2.20 ±0.32 [1.44,3.51] | 2.18 ±0.32 [1.52,3.17] |
| nExCly 0.9 | 6.71 ±2.41 [1.6,18.1] | 5.98 ±2.53 [1.2,13.8] | 7.19 ±3.41 [0.0,15.9] | 9.83 ±3.91 [2.9,23.2] |
| dAN/CS 0.9 | 0.296 ±0.006 [0.283,0.329] | 0.293 ±0.008 [0.273,0.315] | 0.288 ±0.006 [0.276,0.307] | 0.293 ±0.007 [0.274,0.309] |
| PoOc/CL 0.9 | 0.382 ±0.009 [0.359,0.403] | 0.374 ±0.012 [0.346,0.401] | 0.391 ±0.009 [0.371,0.420] | 0.396 ±0.008 [0.374,0.411] |
| EL/CS 0.9 | 0.251 ±0.006 [0.237,0.266] | 0.245 ±0.008 [0.226,0.266] | 0.251 ±0.008 [0.231,0.273] | 0.252 ±0.007 [0.236,0.268] |
| MGr/CS 0.9 [%] | 3.63 ±0.73 [1.82,5.79] | 3.38 ±0.80 [1.58,6.08] | 3.15 ±0.83 [1.50,6.87] | 3.56 ±0.86 [1.54,6.48] |
| MW/CS 0.9 | 0.637 ±0.021 [0.595,0.702] | 0.639 ±0.022 [0.580,0.692] | 0.638 ±0.020 [0.584,0.682] | 0.644 ±0.019 [0.604,0.690] |
| ML/CS 0.9 | 1.301 ±0.035 [1.174,1.392] | 1.300 ±0.029 [1.232,1.379] | 1.278 ±0.030 [1.207,1.356] | 1.297 ±0.029 [1.216,1.373] |
| Fu2L/CS 0.9 [%] | 13.60 ±0.39 [12.60,14.52] | 13.96 ±0.50 [12.84,15.06] | 13.47 ±0.47 [12.24,14.84] | 13.38 ±0.47 [12.49,14.62] |
| IFu2 0.9 | 1.691 ±0.064 [1.537,1.926] | 1.691 ±0.079 [1.491,1.856] | 1.707 ±0.060 [1.556,1.873] | 1.667 ±0.057 [1.517,1.816] |

**TABLE 6.** Morphometric data of males of *Tapinoma madeirense* and *subboreale*. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. The column in between gives the F values and significancy levels of a one-tailed ANOVA.

| | *subboreale* (n=77) | ANOVA $F_{1,100}$, p | *madeirense* (n=25) |
|---|---|---|---|
| ML [μm] | 1508 ±54 [1314,1627] | 1.43, n.s. | 1489 ±84 [1307,1639] |
| SPExc [μm] | 307 ±21 [265,354] | 130.8, 0.000 | 248 ±27 [204,297] |
| SPdT [μm] | 526 ±34 [419,594] | 51.7, 0.000 | 465 ±46 [370,533] |
| SPWPr [μm] | 194 ±10 [170,218] | 1.00, n.s. | 192 ±15 [165,245] |
| dSPST [μm] | 150 ±21 [109,202] | 168.4, 0.000 | 215 ±25 [176,268] |
| SPExc/ML | 0.204 ±0.014 [0.175,0.241] | 110.1, 0.000 | 0.167 ±0.019 [0.133,0.209] |
| SPdT/ML | 0.350 ±0.023 [0.286,0.400] | 41.55, 0.000 | 0.313 ±0.031 [0.251,0.361] |
| SPWPr/ML | 0.129 ±0.007 [0.117,0.145] | 0.001, n.s. | 0.129 ±0.013 [0.109,0.172] |
| dSPST/ML | 0.100 ±0.014 [0.071,0.137] | 160.0, 0000 | 0.145 ±0.019 [0.119,0.193] |

**TABLE 7.** Morphometric data of workers of small *Tapinoma* species with shallow clypeal excision. The data of *T. sinense* are less accurate as they were taken from images. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

| | *T. kinburni* (n=7) | *T. pygmaeum* (n=18) | *T. sinense* (n=3) | *T. sichuense* (n=4) | *T.dabashanica* (n=3) |
|---|---|---|---|---|---|
| CS | 586 ±26 [545,630] | 488 ±23 [443,517] | 673 ±40 [617,710] | 695 ±23 [665,720] | 650 ±20 [628,665] |
| CL/CW | 1.137 ±0.024 [1.087,1.156] | 1.141 ±0.024 [1.103,1.188] | 1.057 ±0.035 [1.016,1.101] | 1.140 ±0.015 [1.126,1.157] | 1.160 ±0.019 [1.147,1.182] |
| SL/CS | 0.924 ±0.013 [0.906,0.949] | 0.846 ±0.019 [0.819,0.889] | 0.903 ±0.012 [0.888,0.918] 2 | 1.040 ±0.026 [1.004,1.065] | 0.991 ±0.004 [0.987,0.994] |
| ExOcc/CS [%] | 0.73 ±0.47 [0.00,1.17] | 1.08 ±0.49 [0.08,2.19] | 0.74 ±0.20 [0.52,1.00] | 0.50 ±0.23 [0.20,0.77] | 0.00 ±0.00 [0.00,0.00] |
| ExCly/CS [%] | 2.96 ±0.30 [2.40,3.26] | 0.55 ±0.34 [0.00,1.04] | 2.76 ±0.45 [2.30,3.37] | 4.84 ±0.13 [4.69,5.01] | 4.38 ±0.18 [4.25,4.58] |
| ExClyW/CS [%] | 8.12 ±0.84 [6.49,8.96] | 11.76 ±2.07 [8.98,16.52] | 10.16 ±1.52 [8.37,12.08] | 7.98 ±0.55 [7.51, 8.75] | 8.38 ±0.39 [8.11, 8.82] |
| ExClyL/W [%] | 0.366 ±0.030 [0.312,0.406] | 0.048 ±0.031 [0.000,0.114] | 0.273 ±0.034 [0.229,0.311] | 0.608 ±0.029 [0.573,0.643] | 0.524 ±0.035 [0.488,0.559] |
| nExCly | 0.43 ±0.53 [0.0,1.0] | 0.97 ±0.92 [0.0,3.0] | 2.33 ±0.47 [2.0,3.0] | 2.00 ±0.00 [2.0,2.0] | 3.67 ±0.58 [3.0,4.0] |
| dAN/CS | 0.303 ±0.005 [0.295,0.309] | 0.323 ±0.009 [0.304,0.337] | 0.314 ±0.010 [0.304,0.328] | 0.305 ±0.006 [0.296,0.309] | 0.300 ±0.004 [0.297,0.304] |
| PoOc/CL | 0.435 ±0.008 [0.425,0.447] | 0.500 ±0.007 [0.485,0.511] | 0.444 ±0.006 [0.437,0.451] | 0.397 ±0.007 [0.387,0.404] | 0.411 ±0.003 [0.409,0.413] |
| EL/CS | 0.273 ±0.006 [0.263,0.283] | 0.244 ±0.006 [0.234,0.257] | 0.285 ±0.011 [0.273,0.300] | 0.284 ±0.004 [0.279,0.289] | 0.298 ±0.004 [0.295,0.303] |

*...Continued on the next page*

TABLE 7. (Continued)

|  | *T. kinburni* (n=7) | *T. pygmaeum* (n=18) | *T. sinense* (n=3) | *T. sichuense* (n=4) | *T.dabashanica* (n=3) |
|---|---|---|---|---|---|
| MGr/CS [%] | 2.47 ±0.38 [2.06,3.13] | 1.57 ±0.44 [0.72,2.47] | 2.94 ±0.82 [2.12,3.76] 2 | 1.84 ±0.37 [1.29,2.04] | 2.58 ±0.94 [1.79,3.62] |
| MW/CS | 0.631 ±0.011 [0.618,0.653] | 0.624 ±0.023 [0.588,0.683] | 0.650 ±0.033 [0.625,0.696] | 0.662 ±0.004 [0.657,0.665] | 0.682 ±0.023 [0.658,0.704] |
| ML/CS | 1.219 ±0.036 [1.174,1.290] | 1.157 ±0.028 [1.119,1.228] | 1.191 ±0.015 [1.176,1.211] | 1.377 ±0.017 [1.356,1.394] | 1.293 ±0.027 [1.263,1.315] |
| Fu2L/CS [%] | 10.18 ±0.35 [ 9.76,10.60] | 8.28 ±0.39 [ 7.45, 9.04] | 11.12 ±0.04 [10.70,11.54] 2 | 12.74 ±0.19 [12.57,12.97] | 12.79 ±0.16 [12.60,12.91] |
| IFu2 | 1.141 ±0.068 [1.042,1.209] | 0.933 ±0.057 [0.842,1.095] | 1.225 ±0.025 [1.200,1.250] 2 | 1.403 ±0.060 [1.313,1.437] | 1.357 ±0.024 [1.333,1.380] |

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